Winter Track Patterns of Snowshoe Hare (Lepus americanus), Red Fox (Vulpes fulva) and Lynx (Lynx canadensis) Related to Distance from Corridors and Habitat Type Near Cochrane, Northeastern Ontario, Canada

by

©Cynthia Jane Davey

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"When someone you love becomes a memory, the memory becomes a treasure."

Abstract

Track distributions of snowshoe hare (Lepus americanus), fox (Vulpes fulva) and lynx (Lynx canadensis) were related to distance from anthropogenic corridors (abandoned road, ditch and hydroline) and habitat types in a disturbed winter landscape near Cochrane, northeastern Ontario.

More hare tracks were found in mature conifer habitat than expected. There were fewer hare tracks in the corridor, in immature conifer habitat and in mature mixedwood habitat than expected. The rest of the habitat types contained hare tracks close to expected values. Fifty-four percent of all hare tracks were found 10 to 30 metres from the centre of the corridor. Far fewer hare tracks were found 0 to 10 metres from the centre of the corridor than expected. More tracks were found 10 to 30 metres from the corridor centre than expected. Distances farther than thirty metres from the corridor centre contained hare tracks close to expected values.

Loglinear analysis indicated that distance from the corridor had more influence on the distribution of hare tracks than did habitat type. The interaction of distance and habitat had an effect as well, but much less so than distance alone. Information analysis also demonstrated that distance from the corridor was more significant to the distribution of hare tracks than habitat type. The distance/habitat interaction was strong as well, with specific distance interval/habitat type combinations contributing much to the observed pattern. The corridor habitat at 0 to 10 metres, mature conifer at 10 to 20 metres, mature hardwood habitat at 10 to 30 and 40 to 50 metres, and mature mixedwood habitat at 20 to 50 metres are specific habitat/distance combinations contributing the most to the observed track pattern. These combinations represent patches which were either avoided or preferentially used by hare, with mature conifer at 10 to 20 metres being used preferentially while the other combinations are avoided.

The sample sizes for fox and lynx were very small (n=30 and 24 respectively). Statistical testing at $p<0.05$ could not reject the hypotheses that fox and lynx tracks were found in distance intervals and habitat types according to availability. At $p<0.1$, analysis showed only that less fox tracks were found in hardwood habitat than expected. However, when the fox and lynx datasets were combined into a single 'predator' dataset, goodness-of-fit testing rejected the hypothesis that tracks were found in distance intervals and habitat types according to availability. However, no variable classes showed significant chi-square values at the $p<0.05$ level. At the $p<0.1$ level, analysis showed that the combined fox and lynx tracks were found in mature conifer habitat more than expected. As well, the combined fox and lynx tracks were found 40-50 metres from the centre of the corridor in less than expected values.

Résumé

La distribution des pistes des Lièvres d'Amérique (Lepus americanus), Lynx du Canada (Lynx canadensis) et Reynauld (Vulpes fulva) ont été un produit de distance de leur corridor d'origines anthropogenique (par example, chemin abandonné, foncé et corridor de l'etricité) et de habitat dans une paysage perturbées du nord-est de l'Ontario. Le nombre de pistes de liévres était plus élevé dans l'habitat des conniferes agées que dans les autres habitats. Le nombre de pistes de liévres était moins élevé dans les habitats de corridor, des jeunes conniferes et des bois francs melangé que dans les autres habitats. Le restant d'habitats containu les pistes de liévres selon leur disponibilité.

Cinquante-quatre per cent des pistes de liévres ont été distribuée dans l'interval de distance 10 - 30 metres de le centre du corridor. Le nombre de pistes de liévres était plus élevé dans l'interval de distance 10 - 30 metres de le centre du corridor que dans les autres intervals de distance. Le nombre de pistes de liévres était moins élevé dans l'interval de distance 0 - 10 metres de le centre du corridor que dans les autres intervals de distance. L'interval de distance 30 - 50 metres containu les pistes de liévres selon leur disponibilité.

L'analyse 'loglinear' ont indiqué que le variable distance ont été un influence plus fort que le variable habitat sur le pattern des pistes de liévres. Aussi, l'interaction des variables distance et habitat ont été un influence plus fort que le variable habitat mais moin fort que le variable distance seulement. L'analyse d'information on indiqué aussi que le variable distance ont été un influence plus fort que the variable habitat sur le patterne des pistes de liévres. L'interaction des variables est aussi plus fort; les combinations specifiques de classes de distance et habitat ont contribuée la plupart de l'information du patterne des pistes de liévres. Ces combinations represente les zones qui sont utiliser ou laissez abandonner par les liévres.

Les samples des pistes de le reynauld et le lynx ont été plus petit. Mais, quand les samples ont été combiner, les analyses ont indiqué que les pistes des prédateurs n'ont pas été distribué en distance ou habitat selon leur disponibilité. Au niveau $p<0.1$, le nombre des pistes des prédateurs était plus élevé dans l'habitat connifere agée que dans les autres habitats. Aussi, le nombre des pistes des prédateurs était moins élevé dans l'interval de distance 40 - 50 metres de le centre du corridor que dans les autres intervals de distance.

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Chapter One. Introduction.

A walk in the woods on a crisp winter day rewards the viewer with an image of animal tracks in the snow, a delicate tracery in white-on-white. These tracks form easily discernable spatial patterns against a matrix of landscape features and vegetation types. How do these winter patterns of wildlife tracks relate to the landscape pattern? Further, in a landscape criss-crossed with linear corridors (eg. cut lines, ditches, roads, etc.), both of natural and human origin, how do wildlife track patterns relate to these corridors as features of the landscape? These two questions form the basis of this dissertation.

Prior to European settlement, the boreal forest was characterized by large stands of lowland black spruce or jackpine sandflats, broken occasionally by upland areas of aspen, birch and poplar. As well, open bogs, burns and blowdown areas added additional structural diversity to the boreal landscape. Fire, windthrow and insect infestations were key disturbance elements.

Yet overall, the boreal forest maintained its characteristic coarse-grained appearance.

However, in the last century increased immigration of white settlers drastically altered the character of the boreal forest. Small-scale agriculture changed forest to open meadows and cropland. Drainage ditches left straightline waterways on the landscape. Mining exploration led to a landscape crisscrossed with gridlines even in the most remote areas. Hydroelectric development along many of the large rivers created long transmission corridors many metres wide across the landscape.

Most significantly, perhaps, forest operations cleared thousands of hectares per year, resulting in a preponderance of relatively small patches scattered within the original conifer matrix. These cuts were connected in most cases by networks of haul roads of various widths, ages and grades. In addition, highly efficient fire suppression and insect control has altered the incidence and spatial characteristics of two of the boreal forest's most potent change mechanisms.

Resulting from these human activities is a landscape no longer characterized by large relatively homogeneous patches in an unbroken conifer matrix. Rather, in many areas the boreal forest is characterized by diverse patches of varying seral stages set in remnants of the original conifer matrix and connected by thousands of kilometres of cutlines and haul roads.

This drastic landscape alteration has significant implications for wildlife. Boreal species have evolved through the millenia to fit the forest's pattern of large-scale catastrophic disturbance followed by succession. Such species fall into three categories: species which require extensive tracts of mature conifer (eg. eastern cougar), species which thrive in newly- or recently-disturbed areas (eg. moose) and species which are adaptable to either condition (eg. black bear). The reason that species are found in certain habitat types and not in others is because the needs of a species are best filled by only a certain type or range of habitat.

Much research has been done into the relationship of wildlife to specific habitat types. From this research, management guidelines have arisen. For example, Ontario's Guidelines for the Protection of Moose Habitat in Timber Management Planning resulted from years of research and observation regarding the various habitat components that moose use throughout the year and the biological reasons for particular habitat use. Species with similar habitat requirements also benefit under the moose guidelines and others like them.

Management guidelines are meant to aid in understanding the habitat components that moose and certain other species need. Required habitat components can then be protected through the medium of forest management planning or sensitive areas management planning. Such planning is used in conjunction with hunting limits to manage populations and habitat for a specific goal, for example increased herd size for more hunting opportunities in the future.

Similarly, guidelines on the habitat needs of raptors and endangered species have been written to assist in identifying and protecting essential habitat for the protection of rare, threatened or endangered species. For endangered species, legislation provides for the protection of key habitat.

Most management guidelines concentrate on the habitat types that certain, usually socially- or commercially-valuable, wildlife species need to maintain their populations at a given level. As well, they have tended to concentrate on habitat types as discrete entities, rather than as integral parts of a larger heterogenous unit--the landscape.

In addition, they have tended to focus on the function these habitat types play in the relationship between population and environment rather than examining their structural relationships. The relation of wildlife and their habitat to human influences is implicit in management guidelines (their purpose is to minimize negative impacts of human activity) but seldom explicitly examined in a rigourous manner.

The spatial pattern of wildlife movement has also been fairly well-researched. Animal behaviouralists and ecologists have noted that wildlife demonstrate spatial patterns of movement, and that these patterns often vary by sex and energetics (Giles 1978), population densities (Smith 1980) and interactions with predators and prey (Giles 1978).

In addition, movement patterns of wildlife also vary with life cycle and seasonality, even time of day. It is also increasingly recognized that spatial heterogeneity in the landscape is important to wildlife (Hunter 1990) and often influences their behaviour, including their movement (Krebs and Davies 1987).

This research project focuses on a few common wildlife species--snowshoe hare (Lepus americanus), red fox (Vulpes fulva) and lynx (Lynx canadensis). These species were chosen because they are ubiquitous boreal forest residents which interact as predator and prey in overlapping ranges. They also exist in sufficient numbers in the study area to yield enough tracks in a short period of time to allow for statistical analysis. Hare particularly are abundant; fox and lynx less so.

As well, fox and lynx are economically important furbearers. Examination of the structural relationship of fox and lynx tracks to habitat patches and corridors may aid in managing these populations and their habitats. Similarly, understanding the relationship of hare tracks to the landscape may aid in management during times of cyclical population extremes, thus benefiting furbearers and the local trapping economy. Understanding how the track distributions of the three species interrelate may aid in managing habitat to optimize their population numbers and thus benefit the local trapping economy.

The project deals with structure rather than function, asking the question 'in what ways do the winter track patterns relate to the habitat types in the landscape, a landscape overlain with corridors of diverse types?' The human aspect of landscape pattern and the reciprocal relations among wildlife, humans and the landscape are also examined.

The answer to the above question is relevant to landscape planning and management. Currently, planning is often accomplished using a rather haphazard mixture of single-species management guidelines and politically-based policies. An extremely amorphous umbrella of concepts such as 'ecosystem management' and 'biodiversity conservation' (difficult enough to define and harder to implement) forms a shaky framework for planning.

In order to manage the landscape with any degree of confidence, a thorough knowledge of species and their relationships with each other and their environment is necessary. This research project aids in this understanding through examining not only individual species' relationships to habitat types and anthropogenic corridors but also their links with each other. In addition, it examines the influences of a disturbed environment in which humans play key roles as change agents.

This type of multiple-species, multi-habitat research in a human-disturbed environment lends itself admirably to an approach grounded in the theories and methods of landscape ecology. Landscape ecology is a field of study concerned with structure, function and composition at a landscape level, i.e. on a scale encompassing many other scales and ecosystems.

At the same time, the field of landscape ecology explicitly acknowledges the human dimension of landscape processes and patterns, offering explanations which encompass both natural and human activities on the landscape. The discipline of landscape ecology can be seen as an integrative field where science and society together provide information necessary to understanding landscapes and their components.

This thesis provides an example of this integrative approach where scientific rigour, experiential knowledge and non-scientific information are brought together in a structured, disciplined manner to illuminate the causes and consequences of observed landscape patterns.

Recently, scientists have increasingly recognized social aspects of the physical and biological environments. However, in the past, most scientific disciplines, including ecology, appear to have largely ignored the human dimension of landscapes, instead concentrating on the relationships of wildlife with aspects of their physical and biotic environments. Humans have been looked at as outside of nature, apart from it, somehow superior to it (Keller 1985). Many individuals hold such a separatist view of nature. Consequently, misconceptions regarding the relationship of wildlife to human disturbances exist.

Social, economic and religious factors complicate the matter. Many people honestly feel that human alterations to the landscape always cause negative impacts to wildlife and their habitat. Relatively few others feel that human alteration of the landscape is inherently beneficial and desirable, creating additional opportunities for wildlife.

Others hold to a stewardship model. Humans are put on the earth to be 'gardeners', to alter the landscape to make it aesthetically pleasing or more efficiently functional. Other 'environmental stewards' feel that humans are morally responsible to 'help' nature, sometimes interpreting this as resisting change in the landscape, particularly catastrophic change (eg. forest fires) or anthropogenic change (eg. logging).

People also hold strong opinions regarding the behaviour of wildlife. Many people feel that wildlife generally react negatively to human presence and human alterations. Such people may feel over-protective of wildlife and extremely negative toward activities which they see as threatening to wildlife, eg. logging and trapping. Human interaction with nature, in this situation, is seen as black-and-white, no shades of grey.

In many cases, such opinions are not informed by experience. People may believe, for example, that wild animals will not go near a human structure on the landscape, eg. road or building. However, someone familiar with both the landscape and wildlife behaviour, eg. a trapper, will say that the best place to find wildlife is near corridors, whether natural (eg. stream) or artificial (eg. roads). Something about these features attracts them.

What is it about these features that attracts (or repels) wildlife? A cursory glance at an old forest road, for example, shows a corridor several metres wide in which only pavement, dirt or grasses are present. Tall grasses, shrubs and tree seedlings crowd its edges, while taller saplings and polewood stand sentinel further back from the open road. Finally, mature trees, the matrix of the original forest, form a seemingly impenetrable wall several metres from the edge of the road.

Clearly, successional forces are at work here. The grasses have colonized the exposed area immediately adjacent to the road. They are followed by shrubs and saplings taking advantage of the opened canopy. A vegetation edge effect, that is, a strip of (usually) young vegetation differing qualitatively from the adjacent original forest, is quite evident. The landscape pattern is altered.

Does this altered pattern affect the location of hare, fox and lynx tracks? Does the corridor itself affect the location of tracks, or is it the newly-available habitat types instead? In other words, is there a distance effect or habitat effect? Or is there a combined distance/habitat effect on the track patterns of hare, fox and lynx? Is one effect secondary to the other? What exactly are the effects and how are they related? Can an 'edge effect' distance be determined for each species? This research project attempts to find an answer for these questions.

Several related hypotheses direct this research:

1. Snowshoe hare tracks are distributed randomly with respect to discrete habitat types located along transects.
2. Snowshoe hare tracks are distributed randomly with respect to distance along transects.
3. There is no difference in the distance and habitat effects on hare tracks.
4. There is no correlation between distance from the corridor and habitat type along transects in relation to hare tracks.
5. All distance/habitat combinations contribute equally to the observed hare track pattern.
6. Red fox tracks are distributed randomly with respect to discrete habitat types located along transects.
7. Red fox tracks are distributed randomly with respect to distance along transects.
8. There is no difference in the distance and habitat effects on fox tracks.
9. There is no correlation between distance from the corridor and habitat type along transects in relation to fox tracks.
10. All distance/habitat combinations contribute equally to the observed fox track pattern.
11. The distribution of fox tracks with respect to distance from corridor echoes that of hare.
12. The distribution of fox tracks with respect to habitat type echoes that of hare.

13. Lynx tracks are distributed randomly with respect to discrete habitat types located along transects.

14. Lynx tracks are distributed randomly with respect to distance along transects.

15. There is no difference in the distance and habitat effects on lynx tracks.

16. There is no correlation between distance from the corridor and habitat type along transects in relation to lynx tracks.

17. All distance/habitat combinations contribute equally to the observed lynx track pattern.

18. The distribution of lynx tracks with respect to distance from corridor echoes that of hare.

19. The distribution of lynx tracks with respect to habitat type echoes that of hare.

20. The distribution of lynx tracks with respect to distance echoes that of fox.

21. The distribution of lynx tracks with respect to habitat echoes that of fox.

The following chapters explain the research project from its theoretical underpinnings through the methods used and presentation and discussion of results to final conclusions and management recommendations.

Chapter Two, Literature Review, provides a critical examination of much of the literature written regarding the habitat needs of wildlife species and the effect of linear features, landscape heterogeneity and human disturbance on wildlife. Chapter Two also gives an overview of the history of landscape ecology as a disciplinary field. Its appropriateness to the research project under discussion is examined.

Chapter Three, Methods, begins with a description of the general region in which the research takes place. The physical environment, including forest cover, drainage patterns, soils, topography and climate are described. A quick social/economic tour of Cochrane, the closest town to the research site, is offered. The importance of logging, trapping, hunting and other resource uses are stressed. An account of the methods used to locate the study sites and a description of the sites themselves follows. Data collection methods and statistical analysis techniques are decribed in detail.

Chapter Four, Results, presents the results of the data analysis. Descriptive statistics, goodness-of-fit, likelihood ratio, correlation, loglinear and information analyses' results are given for hare. Key information drawn from the individual hare trails and trappers' knowledge is presented as well. For fox and lynx, descriptive statistics and goodness-of-fit test results are given by species. The results of the likelihood ratio, loglinear and correlation analyses are also given for fox and lynx.

Chapter Five, Discussion, provides an interpretation of the results, places them in the context of previous research and examines some implications associated with the findings regarding previously-held assumptions about wildlife movement patterns.

Chapter Six, Conclusion, discusses the implications of the findings on forest and wildlife management, both in the Cochrane area and in the larger boreal forest/Claybelt region. Ideas for future research are explored and problems associated with this research project are discussed. Management recommendations are offered.

Full citations for all references are given in References, while the Appendices contain the printed results of the information analysis and diagrams of ten individual hare trails.

There are still so many questions remaining unanswered regarding the relationship between wildlife and the landscapes they inhabit. This research attempts to examine one small aspect of that relationship; namely, the location of animal tracks with respect to habitat type and distance from anthropogenic corridors in a human-disturbed landscape.

"A journey of a thousand miles begins with a single step."

Chapter Two. Theoretical Framework and Literature Review

2.1. Introduction.

Humans are among the few species that manipulate the environment to satisfy their needs for food and shelter. Unfortunately, humans are also the species whose manipulations affect the earth to the greatest degree. Indeed, our own manipulations may prove our undoing as our rate of population growth and our increased technology expand our influence upon the planet. The challenge of our species is to understand the extent and implications of our planet-wide manipulations and to begin to mitigate their effects before we succumb to our own machinations.

Traditionally, it seems that scientists have been loath to involve themselves in the ethics and politics of the world around them, even though they and their research are products of that world (Keller 1985). Too often, studies have been performed in isolation from the anthropogenic factors affecting them as well as without regard for the interactions between the systems of interest and the biotic and abiotic factors influencing them.

This can lead too easily to a blatant disregard for the most basic of ecological tenets: in nature, there are no closed systems. Natural processes do not operate in isolation from the systems of which they are part. To neglect the interaction of elements is to ignore their fundamental features as elements of a whole.

Lately, however, the scientific community has increasingly recognized its links to current and historical social, economic and political environments. Feminists, sociologists and science historians have aided the recognition of science as a social construct, both part of and responsive to societal pressures (Keller 1985, Harding 1986).

The field of landscape ecology, still new and growing, explicitly acknowledges the interrelationships of structure and function at all scales over all time periods in all places and seeks to illucidate these relationships to aid in understanding the nature of the planet. Moreover, the field explicitly accepts that humans are within nature, not apart from it. They constitute part of whatever system is being studied; they are observed as well as observer, and therefore cause effects.

Of course, it is impossible to name, let alone describe and understand, all of the potential interactions among systems. Therefore, it is often appropriate to separate out the elements of interest for further study. The important thing is to recognize the limitations of the study and place it within the context of the greater system of which it is part. Contextualization of systems is a key concept of landscape ecology, blatantly informing every landscape ecological study undertaken.

This chapter begins with a discussion of key features of the field of landscape ecology, then examines key concepts related to wildlife's use of the landscape, including heterogeneity and disturbance, linear features, connectivity and connectedness. Finally, specific studies dealing with the use of landscape features by wildlife (predominately furbearers) will be explored. This will set the stage for the interpretation of results and application to the landscape of interest later in the thesis.

2.2. Landscape Ecology.

This research covers a total study site area of approximately 70 000 m^2, within a study area of about 100 km^2, and ranges over several landscape elements in a disturbed environment, representative of the Claybelt portion of the boreal forest of northeastern Ontario. Therefore, it is deemed appropriate to follow a landscape ecology approach.

There are several schools of thought regarding the field of landscape ecology. The American view of landscape ecology is a "ramification and spatial expansion of population, community, and ecosystem ecology" (Forman and Godron 1986) or "the synthetic intersection of many related disciplines which focus on spatial and temporal patterns of the landscape" (Risser 1987). The Canadian approach is a multi-disciplinary, problem-oriented view (Moss 1987). Finally, the Europeans present a holistic and hierarchical view of landscape ecology as the "scientific basis for the study of landscape units from the smallest mappable landscape cell to the global ecosphere landscape in their totality as ordered ecological, geographical, and cultural wholes" (Naveh and Lieberman 1990).

Landscape ecology focuses on the idea of heterogeneity over space and time (ie. pattern and process), and recognizes the importance of anthropogenic influences on landscapes (Vink 1983), as well as their effect on wildlife habitat and behaviour. Since its relatively recent inception, the field of landscape ecology has drawn upon the concepts and methodologies of other disciplines, particularly geography and ecology, and has synthesized them into a cohesive holistic framework for analysis.

The focus or guiding light behind this synthesis has been the emphasis on pattern in landscapes, its formation and organization, its dynamics and relationship to fauna, its predictability and its response to disturbance.

As Turner and Gardner (1991) note, "the consideration of spatial patterns distinguishes landscape ecology from traditional ecological studies, which frequently assume that systems are spatially homogeneous." Such an assumption has led to the production of models of predator and prey interactions that are not consistent with natural systems. Only when spatial variables are introduced into the models do results more closely mimic natural systems (Sklar and Costanza 1991, McNamara and Houston 1990).

Huston et al. (1988) describe most early ecological models as violating the most basic biological tenet that individuals' actions are inherently local. Instead, most models assume that individuals can be aggregated into homogeneous populations and interact in a similar way. This assumption simplifies the activities and reactions of organisms in a way which leads to a loss of information at every level of analysis.

Landscape ecology provides an ideal conceptual framework for ecological analyses of the movement patterns of wildlife related to corridors and other landscape patches. It offers a compartmental approach to examining relationships by allowing the researcher to consider factors of the environment in the light of 'black boxes' where the inner workings are neglected in favour of the interactions among factors.

Detailed knowledge of all the factors and relationships involved in systems is not always necessary in order to understand the system's functioning (Gardner and O'Neill 1991). As Couclelis (1988) states, "Descriptions of complex systems need not be themselves complex, let alone complicated." Examining a set of chosen variables in the system allows clarification of relationships among these variables. These relationships can then be examined further, and if they prove to be insufficient to explain the functioning of the system then the variables chosen to represent the system need to be re-examined.

Key to landscape ecology is the concept of 'landscape'. Perhaps the simplest definition of landscape is that of Bridgewater (1987): "landscapes are mosaics of patches linked by corridors." Forman and Godron (1986) offer a similar view: "landscapes show a common fundamental structure of patches, corridors, and a matrix."

The key to each definition is heterogeneity. This heterogeneity can be found at any scale; therefore, it is important to define the scale at which one is working, thus delineating the landscape of interest. Some authors use the term 'landscape' in the sense of a large ecosystem, composed of communities, but without examining the role of the non-living environment in the structure and function of that ecosystem.

Other authors insist that landscapes can only be measured at the scale of an aerial photo, for example, covering several square kilometres at a time. A more inclusive view holds that any spatially delineated area can be a landscape if the area is heterogeneous in any structural or functional way. In this case, a moose could be seen as a landscape to the ticks that live on it. At any rate, the important components of a landscape can be seen as heterogeneity in a defined space over a specified period of time.

Weins (1992) conducted a survey on the types of articles appearing in the journal Landscape Ecology and concluded that "landscape ecology is less concerned with theory and hypothesis-testing and more with problems addressing habitat fragmentation, reserve design, biological diversity, resource management, and sustainable development" (in Naveh and Lieberman 1994). Whatever the definition or focus, as Zonneveld (1987) argues, "the study of both the horizontal (chorologic) and vertical (topologic) relationships together is essential for landscape ecology".

Naveh and Lieberman (1990) provide a concise description of the various schools of thought surrounding landscape ecology as well as arguing passionately for a landscape ecology which transcends rigid formalized notions of science and scientific discplinary boundaries to form a new synthesis of knowledge taken from all disciplines, scientific and social scientific, yet used within the common conceptual framework of landscape ecology.

There is merit in this type of holistic approach which attempts to account for all values in a landscape in a systematic way; however, in practice it is very difficult to achieve. Traditional statistical analysis methods limit the ways in which data can be collected. Even the wording of research-directing hypotheses must be chosen to fit the statistical and field collection methods to be used. These methods themselves often dictate the type of research to be undertaken, rather than the other way around.

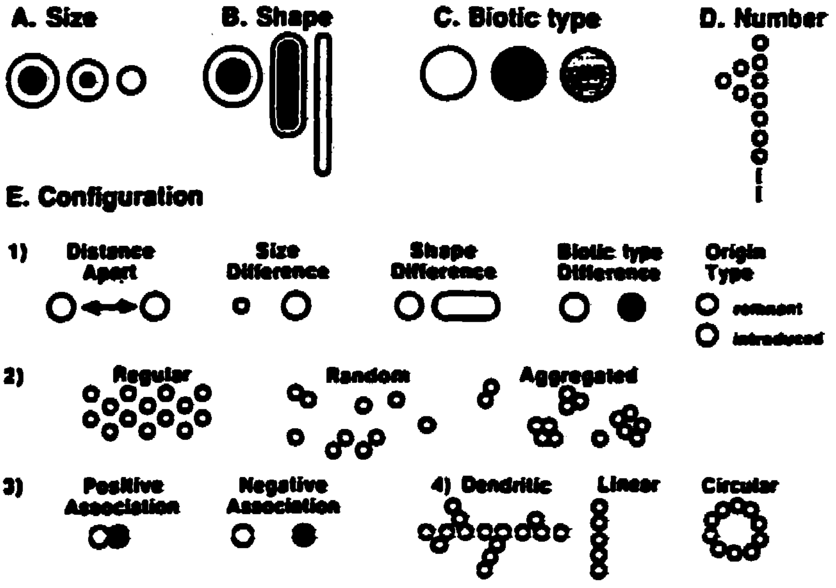
Methodologically, landscape ecology borrows from other fields, and is only now beginning to synthesize quantitative methods into its own body of knowledge (Turner and Gardner 1991). Statistics, particularly those based on probability theory and information theory, lend themselves well to landscape-based analyses. The use of maps and geographic information systems are especially valuable as they yield visual evidence of patterns and relationships. Exploratory studies of spatial phenomena are well-suited to the landscape approach, allowing the researcher to glean what information and patterns may be hidden in the mass of seemingly-unrelated data obtained from field collection.

2.3. Heterogeneity and Disturbance.

The heterogeneity of a landscape directly influences the behaviour and distribution of wildlife, depending upon their species-specific view of the landscape. Heterogeneity in this sense refers to the 'patchiness' of a landscape and is scale- and time-dependent. Heterogeneity may refer to the unequal or 'patchy' distribution of types of resources or habitats or any other element found in the landscape. Patches themselves are varied in their genesis and spatial characteristics (Figure 1).

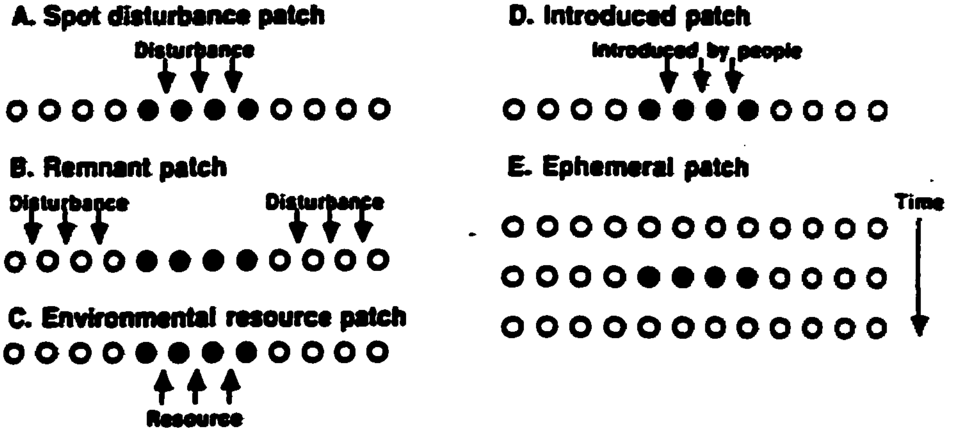
However, heterogeneity must not be confused with 'variability', which is the unequal distribution of the elements themselves across the landscape. Variability refers to one element, while heterogeneity refers to a collection of elements and their structural relationship to each other.

Heterogeneity in a landscape is important to wildlife as it represents different patches available for food and shelter. Many species require different patch types at different times, as



Patch characteristics in a landscape

Figure 1.1. Size and configuration characteristics of landscape patches (Forman and Godron 1981).



Patch origins. Species dynamics within a patch and turnover of the patch itself differ substantially according to the mechanisms causing a patch.
○ ○ ○ = matrix; ● ● ● = patch; disturbance = a sudden severe environmental change.

Figure 1. Genesis and Characteristics of Landscape Patches. (Forman and Godron 1981 in Risser 1987)

diurnal and seasonal changes affect the availability of food and shelter.

For example, moose in the boreal forest generally move from late winter sites in closed-canopy conifer stands to aquatic feeding sites to obtain scarce and necessary calcium-rich aquatic macrophytes during the time in which the nutrients are most concentrated. Often, aquatic feeding sites are close to dense conifer stands which provide cool refuges during hot summer days. Later in the year (autumn, early winter), moose may move to more open, upland areas to feed on aspen.

Johnson et al. (1992) conjecture that animal responses to landscape heterogeneity are a direct result of the animals' movement characteristics, ie. movement rates, directionality, turning frequencies and turning angles in relation to landscape characteristics such as patch type and configuration. They further theorize that such responses alter population dynamics, dispersion and gene flow.

Risser et al. (1984) state that the "dependency of many terrestrial and aquatic vertebrates on habitat mosaics seems to be a general phenomenon." In addition, it has been postulated that the use of many patches by animals essentially 'spreads the risk' in terms of a population's chances for survival (den Boer 1968 in Risser et al. 1984). Each patch in an animal species' habitat carries its own probability in relation to the population's success in surviving to reproduce and so continue the process of evolution. Through the distribution of a population among many patches, the probabilities associated with individual patches merge, effectively lowering the overall probability of population extinction.

In other words, each patch contains a finite amount of a particular resource that the population requires. If that patch's resource is exhausted, the population may survive if another patch with the resource is available. The population, as a collectivity, is not quite so dependent upon a particular patch within its territory if it has access to many patches.

As well, different patch types represent areas which may contain a higher or lower probability of a predator/prey encounter, thus affecting an animal's chance of survival (McNamara and Houston 1990). For example, a hare may encounter a fox more frequently on a corridor than in the adjacent forest. Clearly, there is interaction among animals, habitat patches and abiotic environmental factors. Traditional population-based studies may not adequately account for its complexity.

The importance of heterogeneity to wildlife is illustrated by several studies. Hjeljord _et al_. (1990) found that moose (_Alces alces_) choose foraging habitat based on the nutrient value of the forage. As nutrient value changes during the course of the year, moose move among patches offering optimal nutrient concentration. The role of mature conifer as cover is also discussed. Interestingly, Hjeljord et al. emphasize that moose "interact with forage resources at several levels of ecological scale."

Scale was explicitly defined and identified in their study. As well, landscape-level recommendations were made by the authors, ie. "moose on summer range will benefit from a heterogeneous mixture of plantations and older forest stands", and the human role in the effect of landscape alteration on moose was mentioned.

Ranta et al. (1982) discuss the winter habitat use of wapiti (Cervus elaphus). They found that wapiti use a range of habitat types in winter. Jackpine stands are preferred for basking and shelter from wind. Preferred conifer stands also contain deciduous browse. Travel corridors such as windswept ridges and waterways are also chosen, although the authors do not discuss reasons for this choice.

Wiggers et al. (1992) studied ruffed grouse (Bonasa umbellus) habitat preferences in Missouri and found that grouse density is greatest in 7- to 15-year-old hardwood regeneration. On a landscape level, the greatest density of grouse occurs where such stands comprise at least 14% of the area. Casual observation in the Cochrane area appear to indicate ruffed grouse prefer both mature and immature hardwood for browse (willow, aspen), but that adequate conifer cover is required nearby.

A study by Thompson et al. (1989) demonstrated that fisher (Martes pennanti) use a variety of habitat types for resting, hunting and cover, although deciduous habitats are used less frequently than predicted by availability. The authors attribute the use of several habitat types to the fisher's variable diet.

Disturbance can be defined as "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment" (Pickett and White 1985). Perturbation, on the other hand, refers to a relatively small-scale event from which an ecosystem recovers relatively quickly. Heterogeneity in a landscape affects how the landscape will react to disturbance, ie. to what degree the landscape will resist disturbance ('resistance') or how quickly the landscape will recover from disturbance ('resilience') (Risser 1987; Odum et al. 1987).

Wildlife, as elements of heterogeneous landscapes, also reflect the resistance and resilience of the landscape. In many landscapes (eg. prairie), wildlife (eg. prairie dog) form a significant disturbance force as well (Loucks et al. 1985).

Disturbance regimes play a large role in determining the distribution and behaviour of wildlife (Pickett and White 1985). Freemark (1987) pointed out that human disturbance patterns superimposed over natural disturbance patterns create additional stressors and opportunities for wildlife populations as the landscape is altered in new and different ways. Changes at an individual level may lead to alterations at population, community, ecosystem and even landscape scales over time.

The relatively smaller scale of human disturbance coupled with the increased frequency of human disturbance leads to landscapes composed of large natural disturbance patches in various stages of succession overlain with numerous smaller patches of differing configurations and types. This tends to result in increasingly fragmented landscapes composed of smaller habitat patches isolated from each other by qualitatively different habitats.

Wiens (1985) suggests that habitat fragmentation may lead to the possibility of population extinction, as indicated in Figure 2.

Riewe (1979, 1980) produced two comprehensive and very interesting reports on the interaction of wildlife and landscape

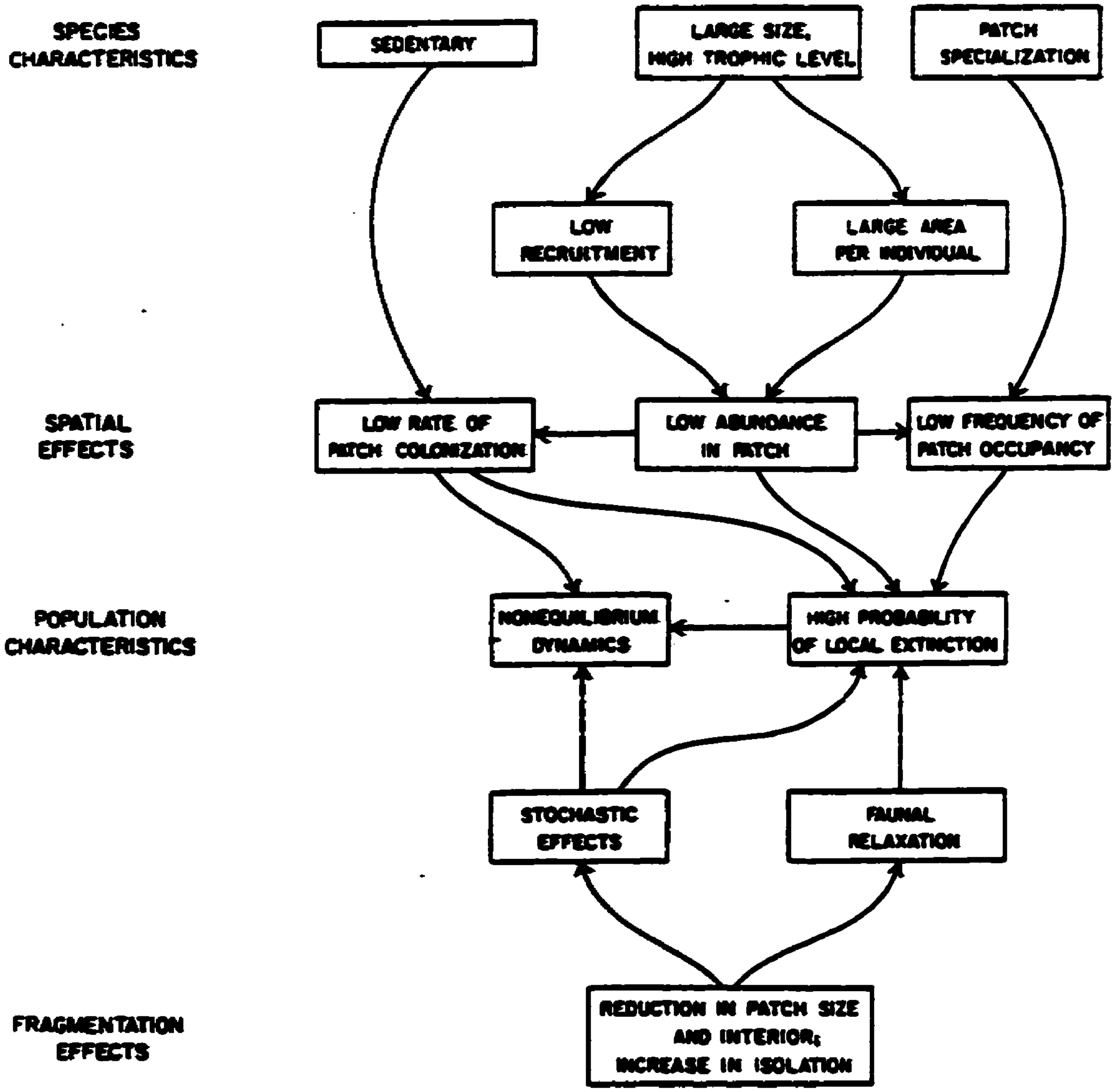


Figure 2. Fragmentation Effects on Local Populations (Weins 1985)

elements in a disturbed environment. Looking specifically at seismic lines, he found that effects were very species-specific and dependent upon an interplay of factors, both biotic and abiotic. His study was particularly unusual in the fact that biotic, abiotic and social factors and their interaction were examined within the greater context of the landscape.

However, landscape ecological theories were not explicitly mentioned in his studies, although one can argue the framework of landscape ecology was used. Riewe's studies can be seen as typical of the Canadian problem-solving, resource management approach to landscape ecology.

2.4. Linear Features, Connectivity and Connectedness.

Much research has been done on the role of linear features in the landscape. Linear features can be divided into natural (eg. streams) and artificial (eg. roads) types. Further, a distinction can be made between 'barrier' (eg. hedges) and 'corridor' (eg. cut lines) features. Barrier and corridor features refer to structures on the landscape, in this sense, and not the function they play with regard to plant and animal movement, since what may form a barrier to some species is a corridor to others and vice versa. Indeed, Bunce and Hallam

(1993) argue that linear features in British agricultural landscapes form important refugia for both plant and animal species, allowing them to disperse into suitable habitat when the opportunity presents itself.

Forman and Godron (1986) further divide corridors into strip corridors and line corridors, with or without breaks (Figure 3). The width, height and composition of strip and line corridors as well as the matrix characteristics can greatly affect the movement of animals across and along the corridors (Figure 4).

Dobrowolski et al. (1993) speak about the effects of habitat barriers such as forest roads and streams in a heterogeneous environment. They argue that such barriers may or may not be difficult for individuals to transcend, but nevertheless form a limit to the movement of individuals as well as forming additional stressors. Additionally, barriers alter the arrangement of habitat patches and may isolate subpopulations. Individuals may also change the shape of their ranges to suit habitat patches affected by barriers.

The authors further argue that predator/prey and other species interactions may be affected by the type and layout of barriers. However, they stress the necessity of defining the effects of heterogeneous landscapes at the species level and

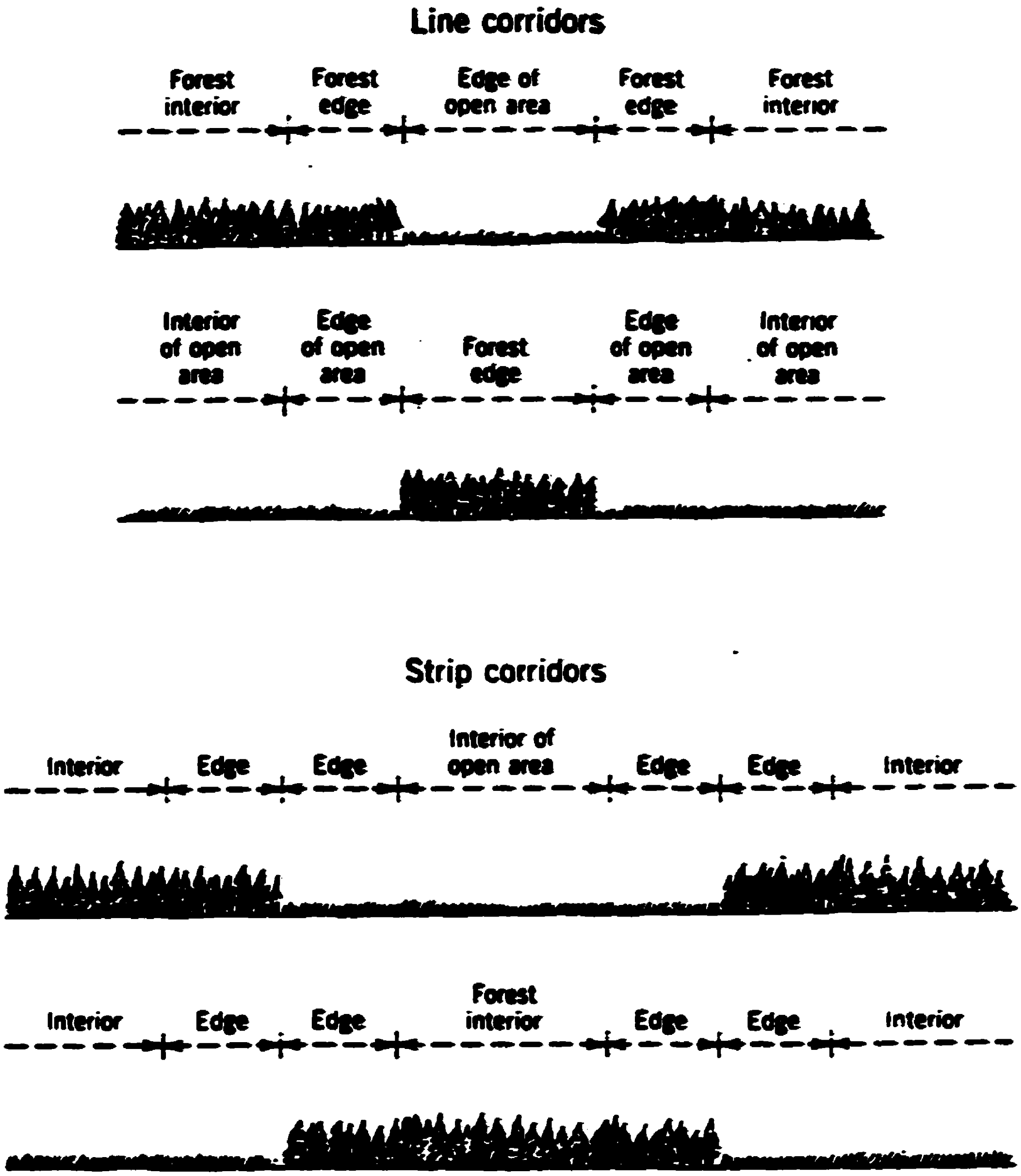


Figure 3. Line and Strip Corridors (Forman 1983 in Forman and Godron 1986)

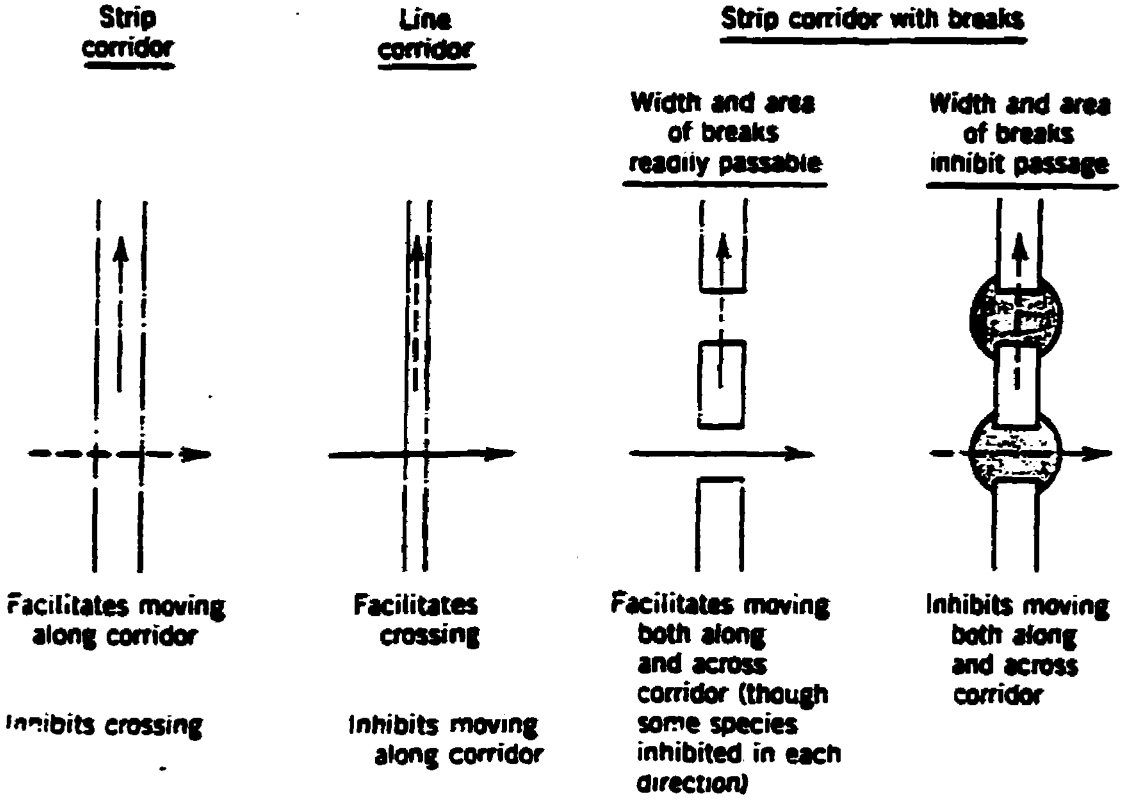


Figure 4. Corridor Effects on Movement (Forman 1983 in Forman and Godron 1986).

("The shaded areas indicate conditions inhibitory to movement and emphasize the critical importance of break areas.")

offer several empirical examples to illustrate the risk of generalization.

Opdam et al. (1993) see linear elements of landscapes both as corridors for the movement of species and as habitat patches in their own right. These linear features function as dispersal mechanisms and suboptimal refugia for species. Depending on their type, linear features may also serve important roles in erosion control, as windbreaks and in water quality and water temperature control (Burel and Baudry 1990).

In addition, Opdam et al. claim that if linear elements occur in heterogeneous environments, they tend to inhibit movement of individuals from one patch to another. The 'spreading-of-risk' effect is suppressed and thus may affect population fluctuations during stressful periods, resulting in populations either more or less resilient to change in the environment.

However, as the authors point out, "very little is known about how individuals actually move through the landscape, whether they use linear elements as corridors, or simply follow a straight or random route, or how they react to boundaries" (Opdam 1991). Indeed, for some species, linear elements may favour, rather than inhibit, the movement of individuals from one patch to another. Again, the postulated effects are undoubtedly very species-specific and, depending upon the environment in which they occur, they may offer both positive and negative effects.

Merriam (1990) addresses the question of animal choice in movement in landscapes crisscrossed with linear features, in this case, fencerows. He finds that white-footed mice (Peromyscus leucopus) "moving through a strange landscape move almost entirely in fencerows. They do not distinguish among several classes of well-vegetated fencerows that the investigators can readily distinguish, but early results show that mice do select wide fencerows as corridors over less wooded and narrower structures." They move to recolonize areas of annual extinction, to locate better food sources and to find overwintering areas.

Merriam uses the term 'connectivity' to refer to the ability of the landscape, through structural features such as fencerow networks, to aid in the movement of subpopulations of a metapopulation. Connectivity then becomes a parameter "which measures the processes by which sub-populations of organisms are interconnected into a functional demographic unit" (Merriam 1984). It also measures interactions of functional processes at a landscape level, eg. nutrient flows (Baudry and Merriam 1987).

Schreiber (1987b) defines connectivity in the broadest sense of "not only the interrelationships in communities and between organisms are meant, but also the network of interactions and flows between the biotic and non-biotic compartments of the ecosystem". In this sense, the term connectivity has a functional slant. As an example, Schreiber demonstrates the role of riparian buffers as regulators of the nitrogen cycle in over-fertilized European landscapes.

In addition, he points out that riparian buffers offer habitat for wildlife as well as a dispersal mechanism. He argues for a land use planning system based on the creation of refugia linked by a connecting network of fence- and hedge-rows, riparian buffers and buffers along other linear features such as roads and the edges of woods.

Forman (1990) uses the term connectivity in a spatial rather than a functional context to describe one of a set of characteristics delineating a 'network landscape'. Network landscapes are characterized by branching networks of fencerows or hedgerows, streams or roads. These networks may or may not connect to diverse habitat patches or elements, as in Figure 5. Importantly, their configuration alone may determine the range of effects, positive and negative, they can have on plant distribution and wildife movement and population dynamics.

As McDonnell and Pickett (1987) point out, the degree of connectivity which a landscape evinces may be of benefit to species in foraging and dispersal, or it may be detrimental and a

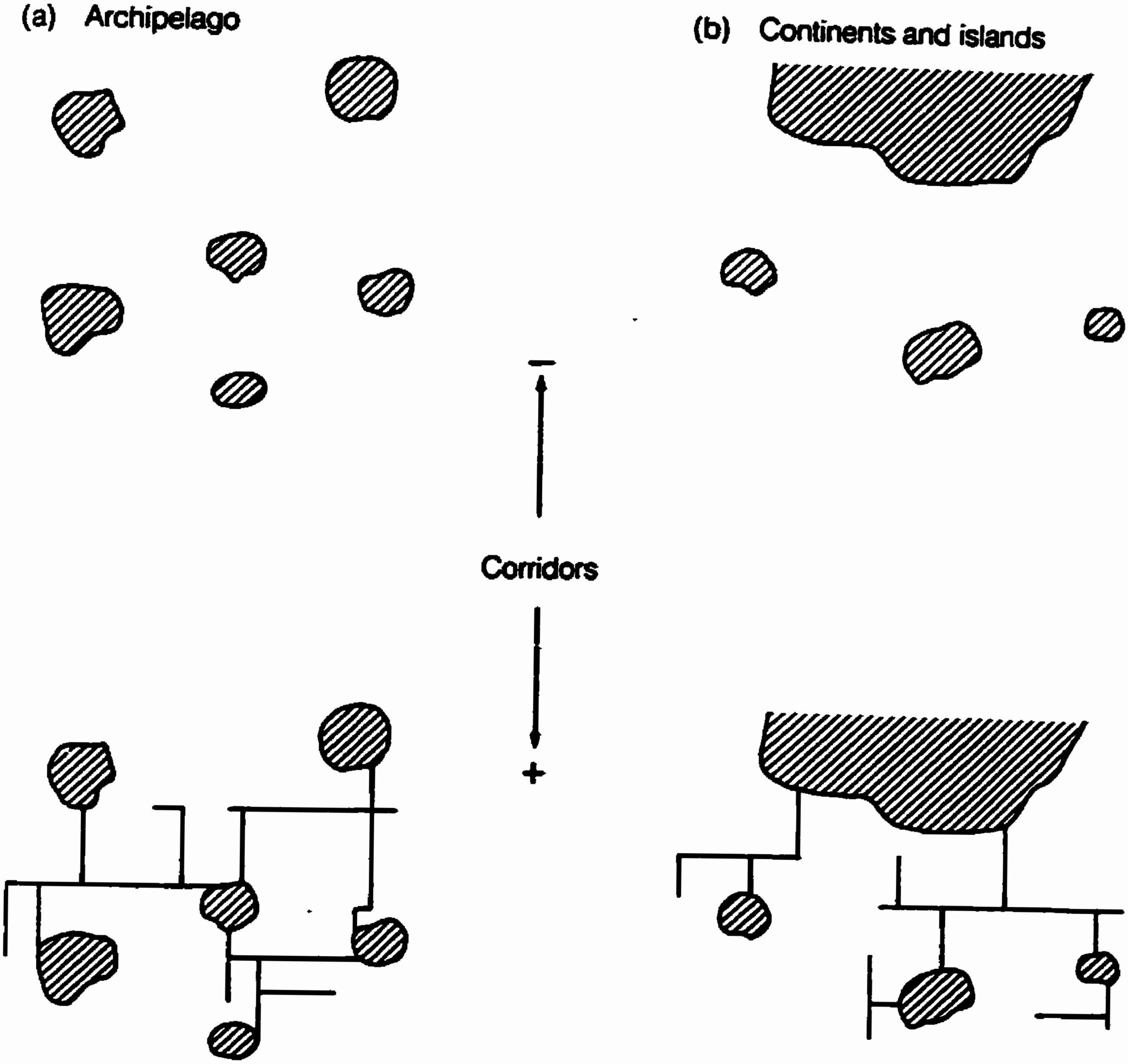


Figure 5. Fragmented Patterns of Patch Distribution with and without Connecting Network (Forman and Godron 1986).

measure of the barriers to foraging and dispersal that exist in that landscape. A third alternative is one of neutrality. It may be that the connectivity of the landscape has no meaning at all to some species--it performs neither a harmful nor a beneficial function. Again, it is important to remember that effects of landscape parameters are both species-specific and scale dependent.

Connectedness is the structural equivalent of the functional concept of connectivity. Baudry and Merriam (1987) define connectedness as referring to "structural links between elements [in] the spatial structure of a landscape and can be described from mappable elements." The degree of connectedness in a landscape is a function of the structure and composition of that landscape and depends upon the number and size of distinct patches in a matrix, the distance between similar patches and the presence and abundance of linear features.

2.5. Species/Habitat/Landscape Relationships.

Plants and animals are directly affected by the environments, biotic and abiotic, in which they live. Particularly, the heterogeneity of the landscapes in which they occur may influence their location and behaviour to various degrees. In a disturbed environment, where natural and/or anthropogenic disturbances cause change to occur extensively or frequently, a species' distribution and behaviour may alter drastically. Or, they may alter only a little but enough to cause long-term modifications. There is also the third possibility that they may not alter at all. Again, the effects are species-specific.

Forman and Godron (1986) define two types of movement: continuous and saltatory. Continuous movement means that an animal moves at either a constant or varying velocity but does not stop over a defined period of time. The example given is of caribou migrating over the tundra. On the other hand, saltatory movement involves stops and starts on the way to a destination. An example may be a snowshoe hare moving in small increments while foraging.

The disturbance of a relatively homogeneous landscape (eg. boreal forest) by extensive human development (eg. road construction) may increase the patchiness of the landscape by creating corridors. This may induce behavioural changes in wildlife, altering movement from continuous to saltatory or increasing the frequency and duration of stops in saltatory movement. In turn, this change may affect survival and dispersal as well as the size of, and movement within, home ranges.

Forman and Godron describe a study by Storm et al. (1976) in which dispersing subadult and adult red foxes (cited as Canis vulpes but more recently named Vulpes fulva) were tracked by radiotelemetry over several years. The study site was located in the northeastern United States in an area of mixed agriculture, woodland and urban development. The results from this study appear to show that foxes avoid buildings, whether single structures or within towns and cities. Additionally, lakes and extremely wide rivers (ie. wider than 55-80 metres) form barriers to fox movement. Forman and Godron also note that:

> One of the most distinctive and surprising findings of the study is that the foxes avoid corridors. None of the foxes followed along the primary landscape corridors such as rivers, major roads, or superhighways (nor did they move parallel to the corridor in the adjacent matrix area). The animals may well have used small dirt roads or paths, but no information is available on this. The avoidance of larger roads is made further apparent by the locations of the daytime beds of these nocturnal creatures. Beds were always recorded more than 92 m away from roads.

Apparently, these types of corridors act as filters rather than conduits, slowing or halting travel rather than enhancing it. Yet despite the filter and barrier effects of these landscape elements, Forman and Godron conclude that "fox movement through the landscape appeared to be generally independent of its structure (at least, as we perceive landscape structure)."

However, the rate of movement through the landscape was markedly affected by highways, lakes, rivers and cities, even if the range of movement appeared not to be. Individuals would approach a barrier, slow their rate of travel and travel in a more erratic manner before crossing the barrier or going around it. Their rate of speed before the barrier was slower than their rate after it. It may be possible that they were intimidated by the barrier and needed to approach the matter cautiously before deciding on a course of action. It may also indicate that they were aware of the existence and location of the barrier prior to actually reaching it, possibly seeing it well in advance or remembering it from past travels. Clearly, the saltatory nature of their travel was altered, increasing both the number and duration of stops.

Forman and Godron also describe a study by Fritts and Mech (1981) to support their discussion of the importance of landscape features to wildlife and the influence of anthropogenic landscape elements on their distribution and behaviour. Several wolf (Canis lupus) packs were studied using radiotelemetry in Minnesota. Farmlands did not appear to affect their movement. However, they readily used roads and drainage ditches in their travels. In this case, wolves appear to prefer these introduced elements which may help them to move around their home ranges more easily and which also form important dispersal corridors.

The importance of particular habitat types in a landscape is illustrated by several studies on wildlife habitat preference. Thompson (1991) demonstrates that marten (Martes americana) require a landscape which contains mature to overmature forest, both conifer and mixedwood. In clearcut and young successional stages, marten are either absent or exist in low numbers, subject to extirpation. If a landscape contains clearcut areas, then the home ranges of marten will be extended to incorporate additional old forest, thus demonstrating that old forest is a necessary component of the landscape to marten.

Soutiere (1979) agrees, finding a significant reduction in marten density in clearcut and early successional stages. Selective cutting does not appear to affect marten density. However, Douglass et al. (1983) raise the question that marten habitat choice may relate more to prey availability than to habitat structure per se. In their study, they find that marten use particular habitats within the conifer forest based on the probability of finding prey rather than on the structure of the forest itself.

Thompson (1991) feels that trapping in mature forest may be a significant cause of local extinction of marten, in addition to direct habitat loss due to forest harvesting.

Casual observation of marten sets, observation of pelts during fur sealing and numerous discussions with trappers in the Cochrane area indicate that trappers in this area usually harvest juvenile marten in second-growth mixedwood stands, often along linear features such as roads and railway tracks.

It is no doubt easier for the trappers this way; however, they strongly believe that it is better for them to trap the juvenile marten and leave the mature marten to reproduce. In this way, they believe, they are taking the 'surplus' that nature provides without harming the reproducing 'core' of the population. It may be that the mature, reproducing marten remain in preferred old forest, while the subadult dispersing marten are left with suboptimal younger habitat. On the other hand, it may simply reflect higher trap susceptibility in juvenile marten.

Thompson et al. (1989) found that fox near Manitouwadge, northwestern Ontario, used 10 to 30 year old stands, while Halpin and Bissonette (1988) report Maine foxes prefer open areas and mixed conifer stands in early winter and mixedwoods in late winter if the snow crusts over. Lindstrom (1982) and Henry (1986) found that fox prefer edge habitats in boreal forests.

Cavanagh et al. (1976) find in a study of selectively-cut, clear-cut and older clear-cut powerlines that the powerline offers different habitat to wildlife depending upon how it was cut and maintained. Firstly, they notice that the selectively-cut area supports more species, particularly forest interior species, while the recently clear-cut area supports less species (predominately edge species). The older clear-cut area supports the least number of species. They also find that even though the powerline may contain desirable forage for snowshoe hare, the use of the habitat is constrained by its distance from cover.

In a similar study, Schreiber et al. (1976) describe the effect of powerlines on small mammals. They find that certain species of voles, mice and chipmunks either prefer the powerline, avoid it or are indifferent to it. The study does not discuss possible interacting effects of cover and predation.

However, an experiment by Doucet et al. (1983) demonstrates this interaction clearly. Conifers (about one to three metres high) were planted in triangles on opposite sides of a 30-metre wide utility right-of-way. Previously, it was found that deer did not use the right-of-way, probably because of its lack of cover from predators and exposure to wind. After the conifer corridor was introduced, the number of deer was significantly greater in the plantation than in the right-of-way.

Deer clearly used these corridors to facilitate crossing the right-of-way.

Not only did deer use the conifer plantings as travel corridors, but they also concentrated their activity in the mature forest near them. Unfortunately, the deer learned late in the study that the planted conifers were a food source and completely destroyed most of them. This may have some implications for the study's findings. At the same time, it demonstrates a clear link between deer, cover and forage habitat.

An earlier study by Doucet et al. (1981) also demonstrates that deer activity is lower in powerlines than in the adjacent forest. Of interest is the fact that "typically, but not exclusively, deer tracks funnelled into runways when they approached the ROW [right-of-way] and fanned out into the forest after crossing it. This pattern, and tracks made by deer which backtracked when they encountered the ROW, accounted for an increase in activity at the woods and ROW interface." Apparently, the powerline produces the type of filter effect defined by Forman and Godron (1986).

A study by Clark and Gilbert (1982) finds that deer appear to select edge habitat but in discussing seeming inconsistencies, they do not mention the filter effect of such ecotones.

Roads appear to produce similar effects to powerlines. A long-term study on brown bears in Norway was conducted by Elgmork (1978) in which it was found that "statistically significant negative correlations exist between the number of bear observations and the density of forest roads."

In a study of grizzly bears, McLellan and Shackleton (1988) found that habitats close to roads are used less than expected. The type of road (ie. primary, secondary or tertiary) and the amount of traffic do not appear to affect the usage.

As well, when bears use areas close to roads, they prefer to do so at night, when darkness offers cover and traffic is lighter. The authors also found that female bears with cubs tend to avoid the areas near roads less than do adult male bears, indicating an avoidance response to the presence of adult males, which are known to prey upon cubs and yearlings. They concluded that the roads themselves were avoided, rather than the habitat associated with roads.

Although McLellan and Shackleton found that roads significantly affect the location of grizzly bears, they found in a later study (1989) that industrial activities connected with seismic exploration do not have an immediate or noticeable effect on grizzlies except to gain their attention occasionally. Key to both of their studies is the explicit description of landscape elements and their role in habitat choice, travel, foraging and predator avoidance. Landscape ecology, as an informing theory, is not stated, yet is implicit in the structure and content of their studies.

Studies of the effects of roads on small mammals have yielded interesting results. Adams (1984) finds that Blarina, Ochrotomys and Peromyscus species are distributed similarly in highway median strips as they are in adjacent areas. Oxley et al. (1974) find that roads of various grades inhibit the movement of small mammals, but that mammals preferring open habitat (eg. Microtus pennsylvanicus) will cross roads more than will mammals preferring forest habitat (eg. Tamias striatus).

A 1983 study by Adams confirms that grassland species prefer road right-of-ways. He also finds that less habitat-specific species appear to use the road/right-of-way/adjacent habitat complex more than would be expected. The variety of species is also greater in road right-of-ways. Mader (1984) clearly shows the barrier effect of roads on Apodemus flavicollis, a forest-dwelling mouse. Figures 6 and 7 effectively demonstrate this effect.

Merriam et al. (1989) found that white-footed mice (Peromyscus leucopus) cross roads infrequently yet their movements near the road are long enough to have crossed the road.

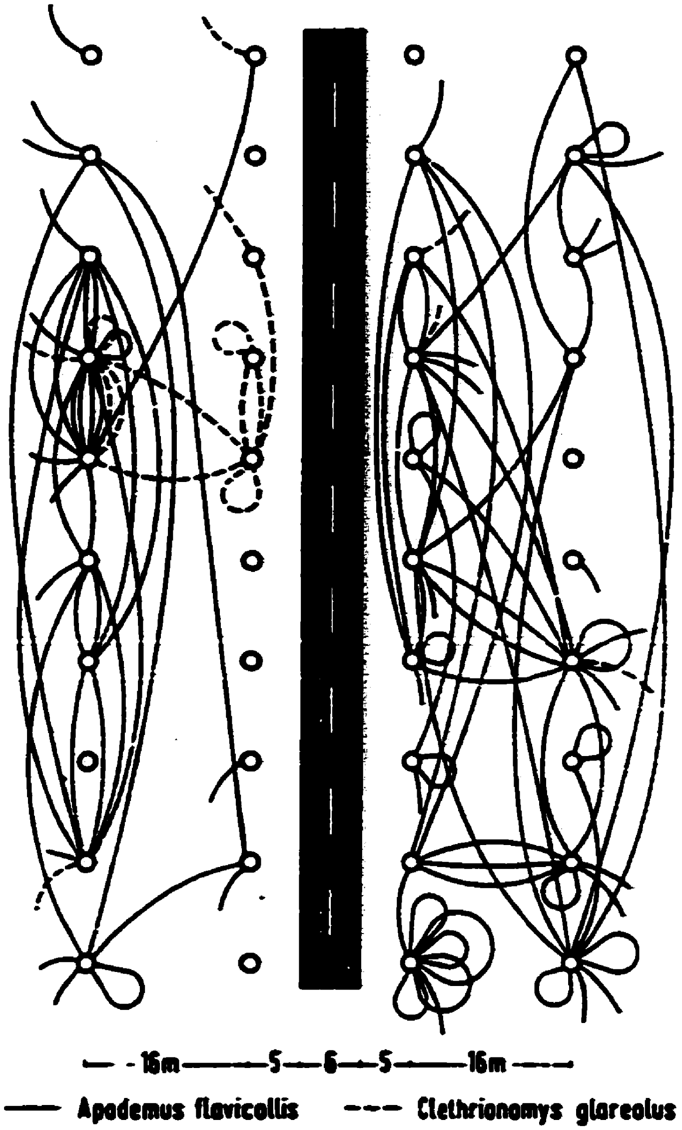


Figure 6. Mobility Diagram Showing Barrier Effect of Road (Mader 1984).

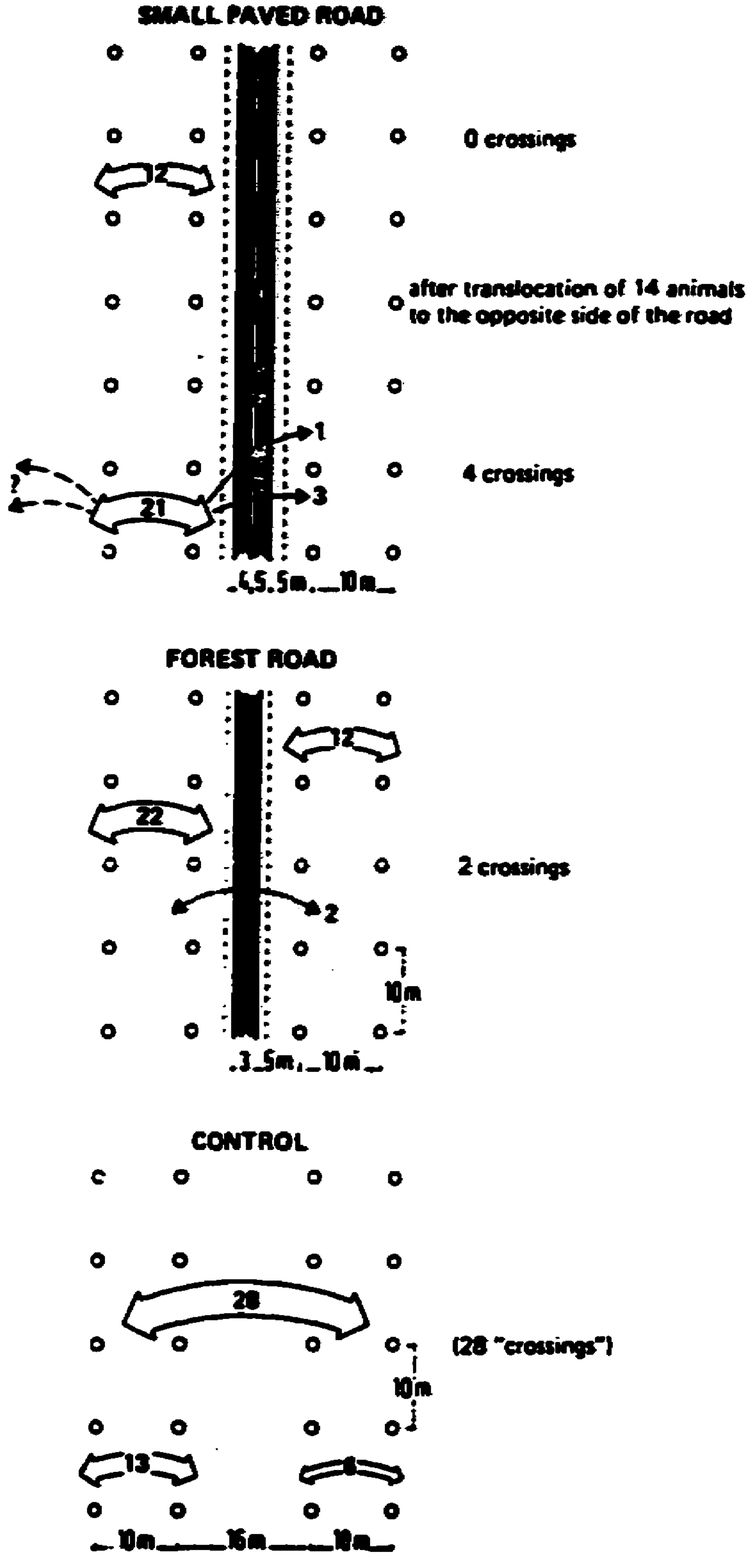


Figure 7. Mobility Diagram Showing Number of Movements Relative to Road (Mader 1984).

Movements near the road are much more frequent than movements across the road.

Winter roads present an interesting type of road for study. Winter roads do not have the same type of gravel or asphalt surface as the roads in the above studies. Instead, they are characterized by grassy vegetation, producing habitat similar to a naturally-occurring grassland or meadow. Douglass (1977) finds that forest-dwelling northern red-backed voles avoid winter road habitat while meadow voles prefer it.

In a study on small mammals in logged areas, Monthey and Soutiere (1985) found that

> overall, small mammal use was greater in partially cut and clearcut softwoods than in uncut softwoods, and greater in partially cut softwoods than in the slash stage of clearcuts. The slash stage received less use by the small mammal community than Rubus or sapling stages of clearcuts. Small mammal activity was greater in uncut hardwoods than in uncut softwoods or the slash stage, and lesser in uncut hardwoods than in partially cut softwoods. Relatively more small mammals were caught in partially cut hardwoods than in uncut softwoods, the slash stage, or Rubus stage.

A study by La Polla and Barrett (1993) found that meadow voles prefer to use corridors to disperse among patches rather than dispersing through the matrix. Henein and Merriam (1990) confirmed that "any connection between two isolated patches is better than no connection at all."

MacCracken et al. (1988) produced an interesting study on the use of habitat by snowshoe hare. In this study, they examined the role of abiotic factors, ie. slope, aspect and elevation, as well as biotic communities on hare habitat use. They found that hare use particular habitats based on relative cover and forage availability. Closed canopy white spruce (*Picea glauca*) stands are preferred as are dense alder (*Alnus* spp.) and willow (*Salix* spp.) thickets. Preferred foods are spruce and willow; alder is not selected as a forage species. This is contrary to a study by Wolff (1978) who found that hare prefer to eat alder and Labrador tea (*Ledum groenlandicum*) as well as spruce and willow.

Casual observation of browsed plants and alder glades in the Cochrane area indicate that alder is neither a preferred forage species nor used for cover. Hare seem to prefer aspen and spruce for forage. Tamarack (*Larix* spp.) are also browsed, particularly during times of high population densities. Dense spruce and immature mixedwood patches appear to be used most for cover.

However, MacCracken et al. warn against making generalizations about hare's use of habitat during times of population highs when suboptimal habitat often contains higher densities. Their study (and my own) was not conducted during population highs, thus avoiding confounding factors due to density.

Further study by Wolff (1980) confirmed his initial findings on the importance of patchy habitats to snowshoe hare. He discusses hare habitat use in terms of an interaction among hare, its vegetation requirements for cover and food and its predators. An explicit discussion of "the role of dispersal in a patchy environment" is also carried out. He found that hare prefer dense stands of spruce or willow/alder in the winter. These species provide both cover and food components. In the summer, hare move to more open shrubby patches to take advantage of the different nutrient composition of these food sources.

However, in times of high hare population, hare will occupy suboptimal patches which may lead to higher mortality in these areas. The patchy composition of the landscape allows hare to move among different patches depending upon time of year and population cycle. As well, Wolff points out that a patchy environment allows hare to select optimal habitat offering both food and cover. These optimal areas function as refugia during times of increased food and predator stress, from which dispersing individuals can emigrate during times of population increase.

Thompson et al. (1989) found that snowshoe hare prefer successional habitat about 20 years old in boreal mixedwood areas. Higher track counts were also found in overmature stands where canopy gaps contain more browse. Parker et al. (1983) also noted that hare prefer 20 year old stands.

Murray et al. (1994) further examine the relationship between snowshoe hare, habitat use and predation, but from the predators' perspectives. Habitat use by lynx and coyote (Canis latrans) in relation to hare distribution and abundance was examined. They found that lynx use open spruce forest and avoid unforested areas; whereas, coyotes use closed spruce forest and unforested areas. In years of low hare density, both lynx and coyote were found in habitats where hare were concentrated, while in years of high hare density, coyotes used habitats in relation to their availability, thus evincing no preference for habitat type. Lynx habitat use did not alter during times of high prey availability.

Murray et al. raise the question that the differing habitat use between lynx and coyote in relation to hare distribution may be due in part at least to an avoidance response of lynx to coyotes. With regard to predation, the authors found that lynx hunt hare in relation to lynx' habitat use, whereas coyote tend to hunt hare more in dense spruce. In an earlier paper, Murray and Boutin (1991) speculate that coyote hunting success is related to its greater foot-load (ie. ratio of weight to foot size) compared to lynx. Deeper and softer snow tend to hamper coyote movement but not lynx.

Thompson et al. (1989) found that lynx prefer successional mixedwood habitats about 20 years old, but were not generally found in mature forest. Parker et al. (1983) also noted that lynx prefer 20 year old stands; however, they were also found in mature forest more often than expected.

Ferron and Ouellet (1992) looked at snowshoe hare's use of summer habitat. They found that hare do not use mature conifer stands or areas with little deciduous understory, preferring instead hardwood and mixedwood areas with canopy closure and herbaceous ground and shrubby vegetation. Dense understory is particularly important to hare, presumably because it offers cover from predators. The authors found that habitat structure was more important to hare than vegetation composition. Small and Keith (1992) related predation of snowshoe hare by red fox to the proportion of dense understory habitat available in a hare's home range.

Keith et al. (1993) examined snowshoe hare survival in a highly fragmented landscape in Wisconsin. They found that hare density appears to be unrelated to patch size, but that extinction takes place more frequently in small patches than in large, unless juvenile ingress occurs. Reproduction rates do not appear to be affected by patch size. However, dispersal success is lower for hare from smaller patches.

2.6. Summary.

Landscape ecology is a rapidly maturing field of study which deals explicitly with landscape heterogeneity and its effects on species. Human disturbance is considered a key element within landscapes. However, as with all relatively recent disciplines, key concepts and methods are still being developed and debated. This makes for a very exciting field of study, yet one which is fraught with confusion and controversy.

The key to understanding the field and its contributions is the same as in all of science. One must define the spatial and temporal scales under discussion and realize that the results of any study, even one designed to illustrate key concepts, is limited to that study. Any attempt to abstract from the specific to the general must be treated with caution until more tests have been undertaken to support or disprove the theories implicit in the concepts. Given these cautions, it is still considered appropriate to use the concepts of landscape ecology to guide this research and the interpretation of results.

Also worth noting is the fact that although many studies specifically dealing with wildlife seek to elucidate relationships between species and their habitat, few do so within a landscape ecological framework. Riewe's work probably comes closest to examining the connections between human disturbance, wildlife and the natural environment. However, his work has been criticized for being too general with a lack of scientific rigour. Even so, it has value as an attempt at a synthetic landscape level examination of relationships among social, physical and biotic elements.

Specific to snowshoe hare, red fox and lynx, the studies examined clearly show a relationship between the species of interest and their habitat requirements within a landscape. However, they also show a relationship between habitat choice and other elements of an individual's life history. There are important links among habitat choice, predator/prey relations, reproduction and dispersal, among others, and these links greatly influence each other. Therefore, it is difficult to separate one from the others without at least acknowledging the existence of these links and their effects on each other.

With one exception, the literature regarding hare does not examine corridors as habitat types within the landscape, nor does it deal explicitly with ecotones. The one study which does examine hare's use of cut line corridors does not examine the effects of the adjacent habitat types nor the effect of distance from the corridor.

The fox literature is sketchy, consisting primarily of a telemetry study relating primarily to large landscape features such as lakes and cities, rather than the smaller features of ditch and narrow road. Other studies examine fox use of habitat in relation to their predation on hare. Of the few studies that exist regarding fox habitat use, none relate in a detailed way to the effects of corridors and their adjacent habitat.

The important link between lynx and snowshoe hare has been well-researched. However, the habitat needs of lynx have not been so well-studied, except in a few studies examining lynx habitat use in relation to the location of hare. One interesting study casts light on the relation of lynx habitat use to predation on lynx by coyotes, leading one to wonder if the location of lynx tracks has more to do with cover rather than prey availability.

As well, very few studies are conducted in the boreal forest, fewer in northern Ontario and none at all in the Claybelt region of northeastern Ontario, which is vastly different in topography, composition and character from the boreal forest of northwestern Ontario. This research project attempts to fill some of the gaps in the literature by explicitly examining the location of tracks with respect to corridors of various types. At the same time, it looks at track distribution according to distance from the corridor and the habitat type present. All of this takes place in a seldom studied portion of the boreal forest, namely the Claybelt region of northeastern Ontario.

The following chapter outlines the methods used in data collection and analysis and describes the study area in terms of its physical geography and socio-economic environment.

Chapter Three. Methods.

3.1. Introduction

This research project was designed to investigate the relationships of snowshoe hare, red fox and lynx track locations to habitat type and distance from corridors in a disturbed winter environment in northeastern Ontario. The patterns of interest in this project exist at the landscape or macro-scale level. However, these patterns are created by the movement of animals, which is in turn influenced by micro-scale factors, like habitat availability, patch type and configuration, snow depth and texture, temperature, etc. In addition, data collection for this project is also at the micro-scale level (ie. on snowshoes). This introduces a problem of scale into the research. Landscape ecology offers tools to deal with different scales.

A line transect approach to the collection of data is one such tool. Sampling of habitat type at each point where a track intersects the transect aids in the elucidation of patterns at the macro-scale even though sampling occurs at the micro-scale. What is sought is the pattern of animal tracks on the transects at specific but unknown time points. These tracks can then be related to habitat type and distance from corridor. Relationships can then be identified through statistical analysis.

In addition to the choices thrust upon the researcher by chance and circumstance, a number of factors were considered when deciding upon the final research location and design. This chapter describes the processes followed for locating the study sites and collecting and analysing data, along with accompanying rationale explaining the decisions reached.

3.2. Study Sites.

The landscape of northeastern Ontario is patchy, with stands of poorly-drained lowland black spruce occasionally interspersed with drier, upland jackpine stands and seral aspen and alder stands. Dotting the landscape are innumerable ponds, lakes, rivers and streams. Recent burns and logged areas increase the heterogeneity of the region, while the intersecting lines of hydro-electric corridors, pipeline rights-of-way, logging roads and railways overlay the landscape matrix. The abundance of logging and mining activities, tourism and recreation and transportation mean that very few spots in the woods are actually quiet. The evidence of human activities is everpresent.

The Cochrane District yields a representative portion of northeastern Ontario's boreal forest. Most of the district is flat, wet and clad in black spruce. On eskers and old beach ridges, jackpine hold sway, while in disturbed areas, alder and aspen/poplar indicate intermediate successional stages. These vegetation classes often occur in discrete stands corresponding to such variables as soil type, drainage and aspect. Stands are fairly accurately mapped in Ontario's Forest Resource Inventory series, allowing the researcher to determine age and species composition of forest stands.

The specific area of study for this research is located several kilometres south of Cochrane (49° 04' N and 81° 01' W) in the Claybelt portion of northeastern Ontario (Figure 8). The area is characterized by poorly-drained lowland black spruce stands with mixedwood stands composed primarily of poplar (<u>Populus tremuloides</u> and <u>Populus balsimifera</u>), white and black

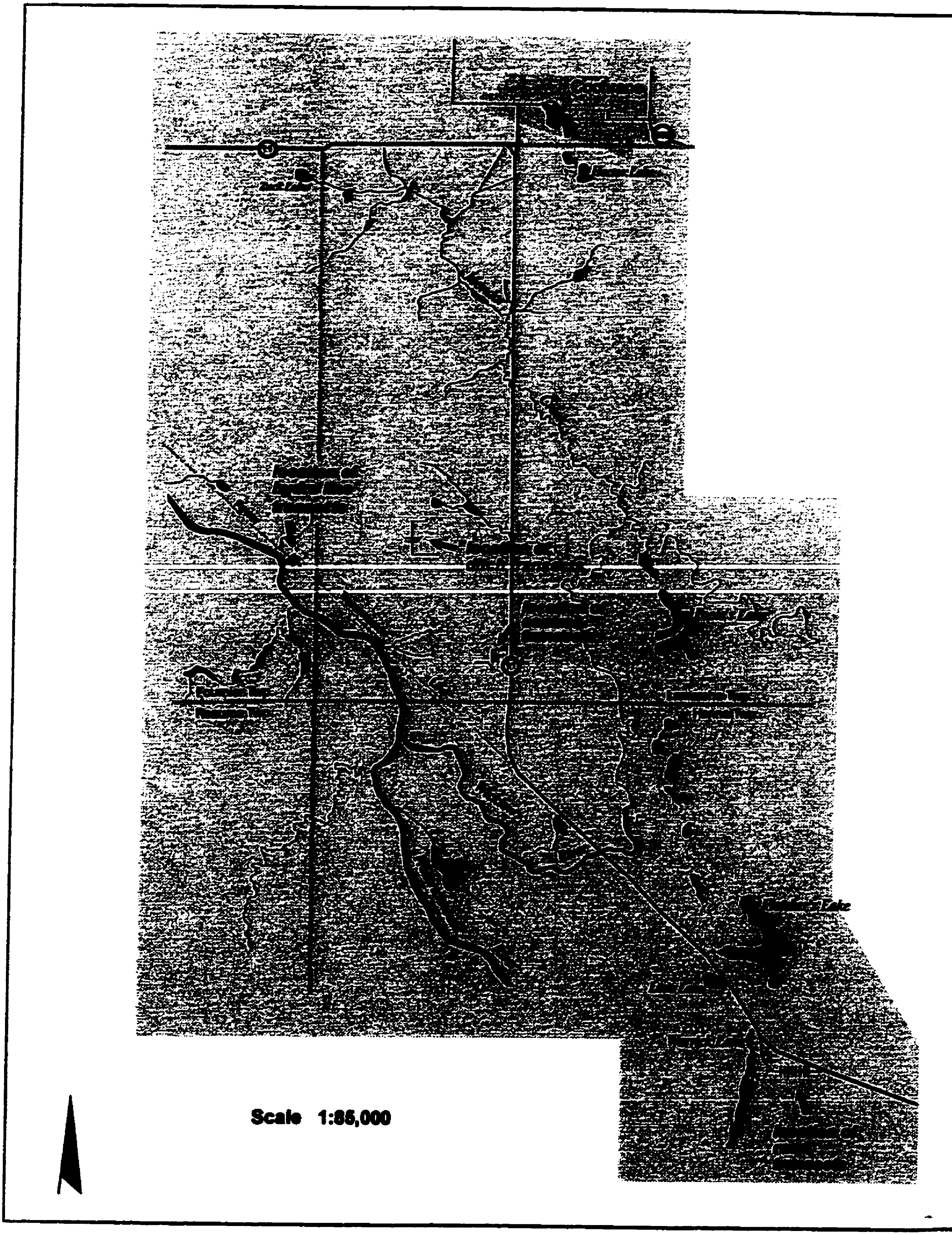


Figure 8. Map of Study Area

spruce (Picea glauca and Picea mariana) and balsam fir (Abies balsamea) on upland areas (eskers, well-drained riparian areas).

The climate is classed as severe mid-latitude subarctic, continental although modified by the presence of Hudson Bay's substantial mass of frigid water (McKnight 1987). As such, the climate is fairly dry with roughly 800 mm of precipitation annually, of which approximately 240 mm fall as snow. Unbroken snowcover exists each year from late October until late March, with a usual maximum accumulation of about 60 cm. The average annual temperature is about 5 degrees Celsius with an average January temperature of -17 degrees Celsius and average July temperature of 16 degrees Celsius. Daytime temperatures in summer rarely rise above 30 degrees Celsius. Nighttime temperatures in January and February regularly reach below -40 degrees Celsius for extended periods of time with accompanying wind chill factors.

Soils are comprised of glacial tills and lacustrine clays over bedrock. In lowland areas, soils are overlain by tens of centimetres of organic material. Elevation is about 900 metres above sea level. The area receives in excess of 1600 hours of bright sunshine a year, with between 160 and 200 days with precipitation (Matthews and Morrow 1985). There are about a thousand growing degree days and between 60 and 100 frost-free days per year. The area is located in zone 2b of the United States Department of Agriculture plant hardiness zone map. Root crops such as potatoes thrive in the clay soil.

Cochrane is a town of (officially) 4500 people, with a diversified economy consisting primarily of logging, pulp production, tourism and a fairly well-developed services sector. The area has been settled by non-natives for almost a century. Before white settlers arrived, native bands lived and traded along the Abitibi River. Evidence of nearly a thousand years of native life exists in several archaeological digs in the area and in the memories of local elders of the New Post First Nation. The Hudson Bay Company was active in the area in the last century, closing their last local post in about 1920.

Hunting is an important recreational and economic pastime, while trapping occupies a significant portion of the local economy and lifestyle. The logging practices in the area co-exist with both of these activities and do not appear to have negatively affected them, or much of the wildlife species upon which hunting and trapping depend (caribou and cougar being exceptions).

Indeed, the forests surrounding Cochrane support several important local industries. Within the Ontario Ministry of Natural Resources' Cochrane Administrative District

> there are two paper mills, two sawmills, and a plywood manufacturing plant. These industries plus their associated woodlands operations employ a total of approximately 2,500 persons. Approximately 1,134,000 m^3 of conifer and 345,000 m^3 of hardwood are cut annually. Generally, there will be a sufficient wood supply to meet the demands for the next 20 years, although localized shortage problems may occur.
>
> Cochrane District has an estimated population of 3,600 moose, of which approximately 7% are harvested annually. The black bear population is estimated to be 1,000 animals with an annual harvest of 80-100 animals. A low density of woodland caribou are [sic] to be found in the northern section of the district. There is no regulated hunt for these animals and Native harvest is quite low.
>
> Big game harvests generate an estimated $1,000,000.00 in revenue annually to the local tourist industry as well as $50,000.00 to the provincial treasury in revenues from licence sales.
>
> Approximately 3,200 beaver, 1,500 mink, 300 weasel, 300 fox, 600 muskrat are harvested annually. The total revenues generated from sales is approximately $180,000.00 annually. [information provided by OMNR Cochrane District dated 1991]

The Cochrane area was chosen as the research site because of ease of access for the researcher and familiarity with the area, as well as for the important intersection of hunting, trapping and logging activities it offers. In addition, the area is crisscrossed with corridors of all types, all readily accessible with snowmobile and snowshoes.

This research project is concerned with wildlife track patterns in disturbed landscapes. Most of the Claybelt area of northeastern Ontario's boreal forest has been disturbed historically by human activity. The face of the landscape has changed remarkably, from a pattern of large relatively homogeneous patches to one in which the original matrix is modified and overlain with numerous smaller, qualitatively different patches and networks of corridors. Consequently, study sites incorporating typical patch types and corridors were sought. Sites were to be in disturbed areas but easily accessible on snowshoes. A control site relatively free of disturbance was also sought for comparison.

Green (1979) recommends this stratified approach for sampling large-scale environmental patterns as it limits among-site variation. The landscape is stratified into relatively homogeneous subunits according to defined criteria, in this case, topography and corridor type. Cochran (1977) also recommends stratified sampling for autocorrelated populations where observations can be expected to be more alike when they are close to each other rather than apart. Hare tracks can be logically assumed to conform to this assumption.

Four study sites were chosen based on landscape composition and the presence of corridors:

1. an intensively-sampled site ("road transects"),
2. an upland site ("hydroline transects"),
3. a lowland site ("ditch transects"), and
4. a control site ("control or bush transects").

The intensively-sampled site is located approximately 20 km south of Cochrane. It is accessible from Highway 11 and contains second-growth conifer, hardwood and mixedwood stands about 70 years old as well as virgin 135 year old conifer. An abandoned, asphalt-surfaced highway (the old Matheson highway) crosses the site (Figure 9) and forms the corridor habitat for this site. Successional forces are at work, slowly reclaiming the old road and eroding the pavement. The corridor is about 6 metres wide. The site is located about 100 metres in from Highway 11. Fourteen 50-metre long transects were located at this site.

The upland site is accessible from the Concession 3 and 4 Lamarche township road and is located about 200 metres in from

Figure 9 . Photo showing Old Highway at Intensively-Sampled Site.

the road. This site consists of second-growth poplar with some white spruce and balsam fir, about 55 years old, and is situated near the shore of the Frederickhouse River. Deeply incised stream and drainage channels cross this site. The corridor consists of a hydroelectric power transmission corridor (Figure 10). This corridor is much wider than the rest of the corridors at about 16 metres wide. Seven transects were located here.

The lowland site is also accessible from the same concession road and consists of second-growth black spruce of about 55 years old with a drainage ditch bisecting the site (Figure 11). The corridor is about 6 metres wide. The site is located about 50 metres in from the road. Four transects were located here.

The control site is composed of mixedwood poplar/black spruce stands about 50 years old and pure black spruce stands about 120 years old (Figure 12). It is accessible from Highway 11 as well. The site is situated about 200 metres in from the highway. Three transects were located here. The control site is located on private land to minimize disturbance, while the other sites are on Crown land and were used for snowmobiling, hunting and trapping during the time of the study.

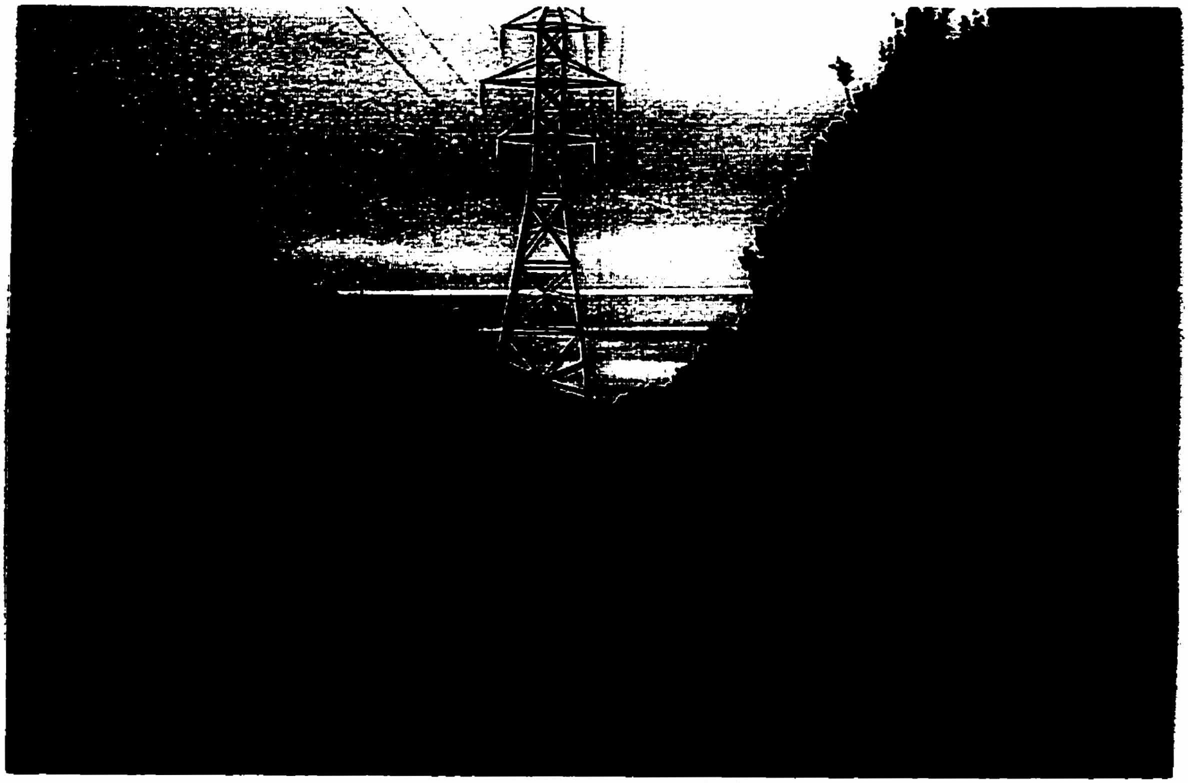


Figure 10. Photo Showing Hydroline at Upland Site.

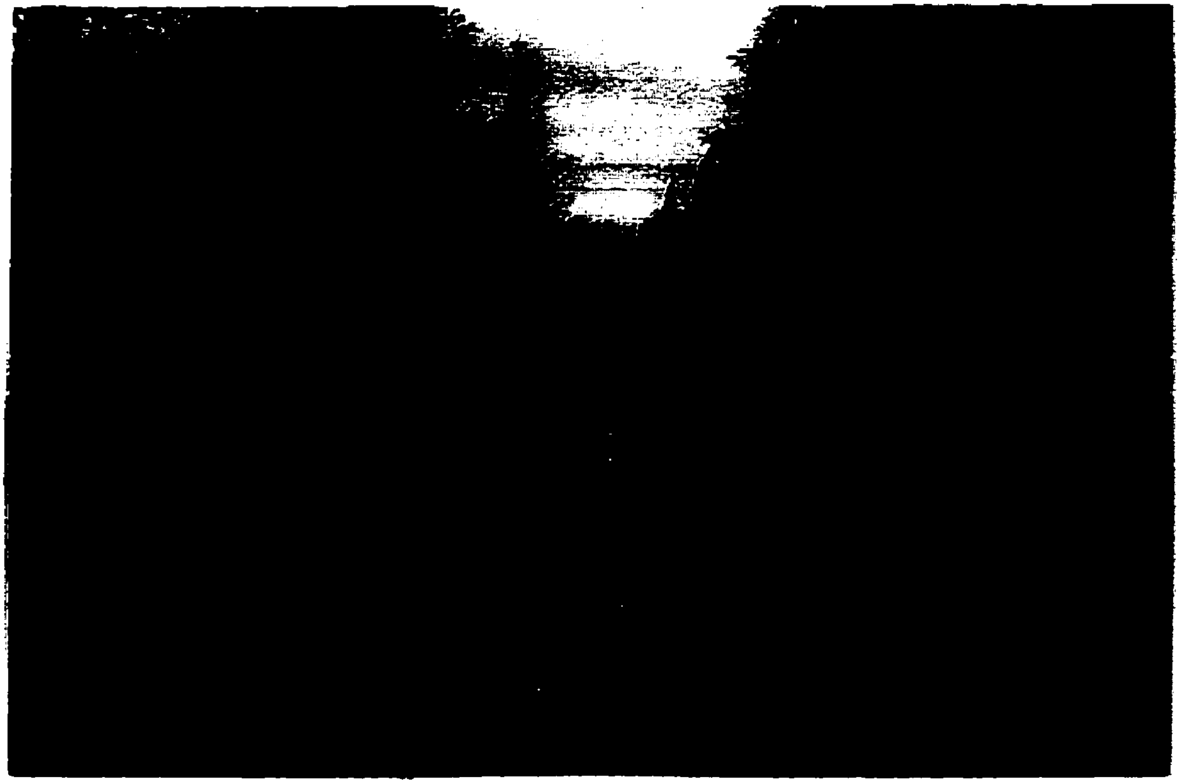


Figure 11. Photo Showing Old Ditch at Lowland Site.

Figure 12. Photos Showing Control Site.

The soils at all sites are humisols and humic gleysols with relatively poor to poor drainage.

Permanent line transects were located perpendicular to each corridor at each of the above sites. Line transects are recommended by Smith (1980) because the method is "rapid, objective, and relatively accurate." It is particularly useful for noting change in vegetation. For animals, it is important to limit the duration of transect studies because of the effects of extraneous factors, such as weather or population cycles (Thompson et al. 1989). This study was limited to one winter (four months - January through April, 1992) for practical purposes.

Snow track surveys using line transects have been used by Douglass et al. (1983), Doucet et al. (1981, 1983), Riewe (1979, 1980) and others. Doucet and Bider (1984) used a sand track survey of line transects through experimental corridors to examine activity, while Clark and Gilbert (1982) and MacCracken et al (1988) used line transects to count deer and snowshoe hare pellets respectively. Snow track surveys are particularly effective in northern Ontario because the long winters, dry cold and little snowfall combine to aid in data collection. The frozen ground makes movement in the bush much easier, while the dry, crisp snow shows tracks clearly for a longer period of time.

Additionally, a track survey yields a large sample compared to, for example, a radiotelemetry sample. Although it may not be as precise as using radiotelemetry, a track survey may be more representative of the species involved since there is a larger number of individuals of each species in the sample. As well, the track survey takes into account several interacting species as well as the space they interact in. Most telemetry studies concentrate on only one species at a time.

The beginning of the transects corresponded to the centre of the corridors. These became the zero metre marks, so that transects stretched 50 metres (or 75 metres for hydro corridors) to either side of the corridor, with the corridor occupying the first several metres of the transect. Transects were 50 metres long for all sites except the transects along the hydroline, which were 75 metres long to adjust for their wider corridors (16 metres versus 6). Length of transect was chosen to reflect the range of distance-influenced habitat in the vicinity of corridors. Several authors have shown that edge effect for vegetation, although species-specific, can be shown to be negligible beyond 10 - 30 metres into the forest (see Wilcove et al. 1986). Luken et al.'s (1991) study of power-line corridors considered 10 - 20 metres within the forest to be interior forest.

Transects were placed 50 metres apart along the length of the corridor, with the first transect located randomly in the site. Hughes (1962, in Southwood 1971) recommends this approach for aggregations such as animal tracks. Similarly, Cochran (1977) recommends this form of systematic sampling for clustered sample subunits in a stratified sample as it offers a gain in efficiency without a loss in precision.

Fourteen transects were placed in the intensively-sampled site (road); seven were placed on the upland site (hydroline); four were placed on the lowland site (ditch); and three were placed in the control site, resulting in a total of twenty-eight transects. Each transect was marked at the corridor edge by two rows of orange flagging tape to aid in locating them later (Figure 13).

Although no flags were removed during the four months of the study, most were removed sometime during the next year, probably by the local trapper or by snowmobilers. This made it difficult to locate transects in following years. This behaviour is unusual in the area since most locals know the importance of leaving flags untouched. The forest is liberally marked with

Figure 13. Photos Showing Flagged Transects.

flags from trappers, loggers and recreational users. In the future, it is recommended that permanent transects be marked with paint rather than flags.

3.3. Data Collection.

It was felt that an observational approach to this research project would be more useful than an experimental/manipulative approach, for several reasons. Firstly, very few assumptions are made in observational research relative to experimental/manipulative research. The researcher records what is made apparent to her/him over time. The results of such research may or may not result in clear relationships among factors. However, they will identify factors upon which to base further research to test relationships among those factors.

In that sense, observational research provides both baseline data for further research and a preliminary exploration of phenomena in order to ascertain possible relationships for further study. In the case of this project, such observational research resulted in the identification of strongly-related factors which will form the basis for future research into the pattern of animal tracks in winter landscapes.

Finally, because this research project is essentially a landscape-based one, experimental/manipulative approaches are quite difficult due to the large space involved and the interplay of a myriad of extraneous factors, such as mortality, migration, hunting pressure, etc. Such factors may not be of significance in an observational study carried out in a relatively short time span; however, over a longer period of time, they may interact to alter the patterns of the environment, including those under investigation.

Data collection for this project consisted of snowshoeing each transect at least twice, during the period January through April. The intensively-sampled and control sites were sampled from two to five times, while the upland and lowland sites were only sampled twice. The upland and lowland sites were sampled lightly primarily in order to determine whether the track distribution echoed that of the intensively-sampled area. If there were no significant difference, then one could assume that different types of corridors affect track distributions in similar ways. Thus, all the transects' data could be lumped together for analysis, enlarging the sample and applying the findings to a broader area.

Sampling occurred within several days after a snowfall, so that the same tracks were never counted twice. Transects were divided into ten-metre intervals from the centre of the corridor (representing the zero mark). The number of track observations for each species per distance interval was recorded. When tracks followed the snowshoe trail for any distance, the point where the animal first entered the transect was used.

Hare, fox and lynx all followed the snowshoe trails occasionally, probably because the packed snow was easier to travel on (Figure 14). It is not believed that this tendency biases the results very much because, although the snowshoe trail was crooked, the transect remained straight. The tracks on the transect did not appear to be much influenced by the snowshoe trail.

At the same time, the dominant habitat type for each distance interval was also recorded. Habitat type was based on a combination of overstory and understory vegetation and characterized into seven classes:

1. edge (corridor, grass, alder, immature trees)
2. immature conifer
3. mature conifer
4. immature hardwood
5. mature hardwood
6. immature mixedwood
7. mature mixedwood

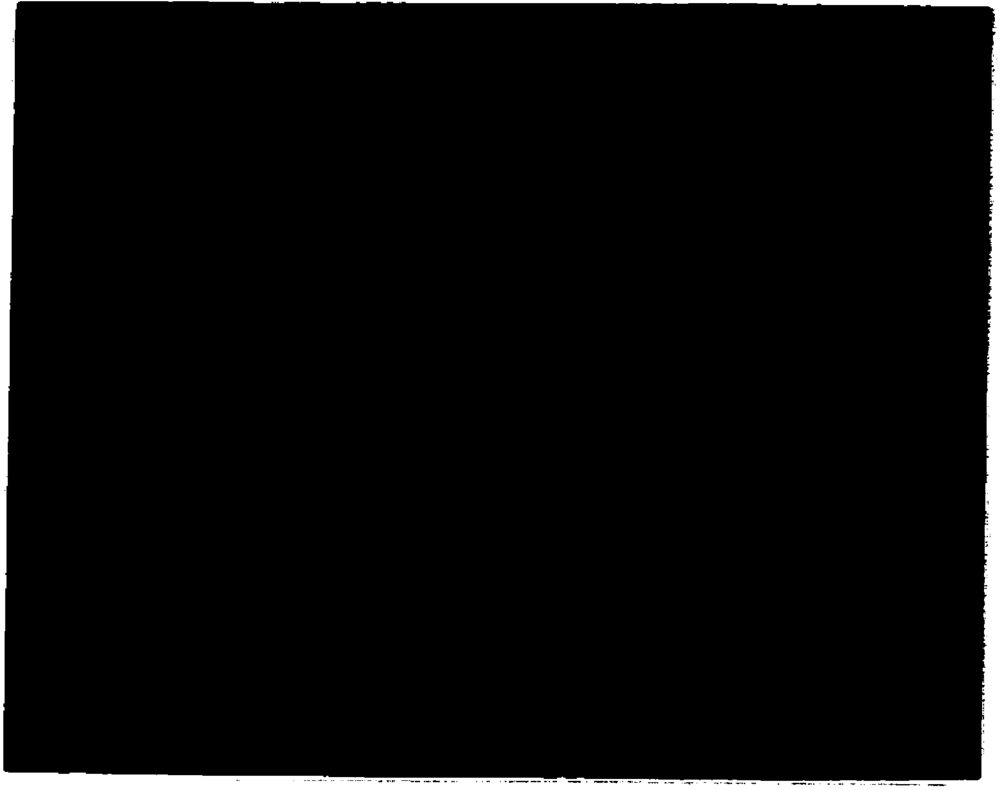


Figure 14. Photo Showing Fox and Hare Tracks Following Snowshoe Trail.

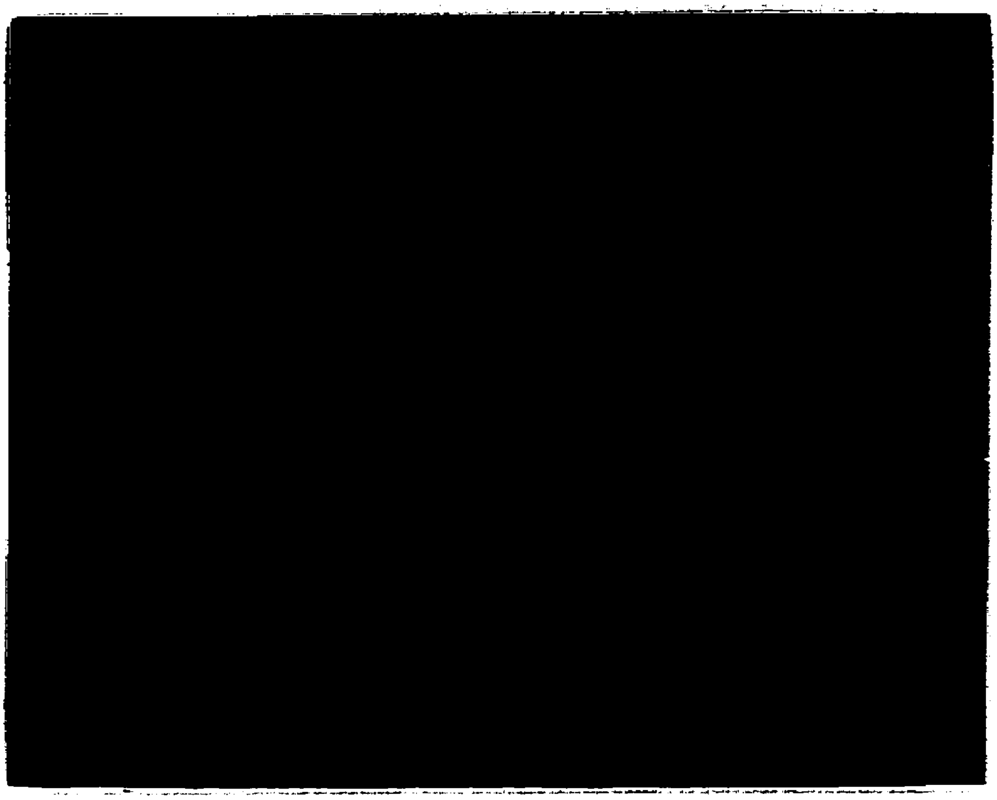


Figure 14a. Photo Showing Lynx Tracks Following Snowshoe Trail.

The above data collected was of sufficient quality to be analysed statistically. However, it was also felt that additional qualitative information could be used to aid in interpreting the results of the statistical analysis. Hence, interesting observations, eg. browse utilization, animal behaviour, animal sightings, etc., were recorded as well.

In addition, ten individual hare trails were followed, independently of the transects, for an interpretative comparison. Trails were marked on graph paper, with each square representing one square metre. Habitat types were mapped on the graph paper as well. These rough diagrams were then translated into line diagrams using Microsoft Windows' Paintbrush function.

In order to illuminate the findings still further, local trappers were questioned informally about their understanding of hare, fox and lynx habitat use and relationship to corridors. Many of the Cochrane area trappers have decades of experience, and it was felt that a comparison between their experiential knowledge and the results of the data analysis would be interesting in itself and could point out inconsistencies and areas for further research.

3.4. Data Analysis.

All observations were input into a database, using DOS Editor. The database contained 848 observations organized in columns of 'date', 'species', 'transect', 'distance' and 'habitat'. This was imported into Dbase III+ for quick searches and rearranging the data. However, the DOS file was used for statistical analysis. It was imported into SAS for descriptive and multi-variate analysis. SAS has a number of procedures which easily sort and analyse data based on the column (variable) titles. The following output was produced by SAS:

1) Graphs and tables of frequency of track observations by distance interval and habitat type along with corresponding descriptive statistics for hare, fox and lynx;

2) Contingency tables of distance by habitat along with corresponding likelihood-ratio chi-square values for each species;

3) Correlation analysis for each of the above; and

4) Loglinear analysis for each of the above.

The Shapiro-Wilk test was performed to test for normalcy of the data. The power of this test in detecting departures from normalcy is excellent (Zar 1984). Variances, skewness and kurtosis were determined for each transect and for the pooled dataset. The Kruskal-Wallis test of homogeneity was performed in order to justify lumping transects. The test of homogeneity allows one to determine if samples can reasonably be expected to come from the same population (Jelinski 1991), thus can be pooled to obtain a larger sample (Zar 1984).

Goodness-of-fit tests were performed to determine whether track distributions occurred in proportion to habitat availability and distance interval. They were also used to test whether the track distributions of fox and lynx echoed each other and that of hare. The likelihood-ratio test was used to indicate whether the variables Distance and Habitat were independent. The likelihood-ratio test approximates a chi-squared distribution but is not constrained by expected cell values of less than five (Jelinski 1991).

Correlation analysis was done to test for associations among variables, ie. "the amount of variability of one variable (either Y or X) accounted for by correlating that variable with the second variable" (Zar 1984). Spearman's rank-order correlation was calculated as appropriate to nonparametric data.

Loglinear analysis was also performed to ascertain the strength of interactions between variables. Such models are useful where variables are not divided into response (dependent) or explanatory (independent) (Wrigley 1979). According to Wrigley, the "loglinear model approach to the analysis of cross-classified categorical data involves the fitting of a set of. . .models to the observed contingency table data and the selection of one of the models as the most acceptable on the basis of its goodness-of-fit, parsimony and substantive meaning." The goodness-of-fit is tested using the log-likelihood ratio. Twice this quantity gives the *G* statistic which approximates the chi-square distribution but is not subject to the same limitations (ie. when expected cell values are less than 5). Loglinear analysis is appropriate in situations where $|f_i - \hat{f}_i| < \hat{f}_i$ (Zar 1984).

An information analysis was performed to define further relationships between the variables Distance and Habitat, in relation to the track distribution, in order to determine which variable contributes most to the observed pattern. Information analysis is nonparametric, ie. free of assumptions of normalcy, and is also void from any effect of correlation of variables.

A software program, PEGASE, based on information theory and developed by Michel Phipps (1981a), was used in this analysis. In a divisive, stepwise fashion, PEGASE calculates the mutual information brought by each class of the variables and groups together those sets that contribute the most to the information contained in the observed pattern. Each subset so formed is subjected to the same procedure until stopping rules end the process. This results in sets grouped according to the classes which provide the greatest relative mutual information, ie. those classes which contribute most to creating the patterns in the landscape.

PEGASE has been used successfully to aid in developing an Ecological Land Classification (Davis and Dozier 1990), to study the relationships between land use systems and soil characteristics in the rural landscape (Dumanski et al. 1987) and to identify ethno-linguistic influences on the landscape in Ontario and Québec (Phipps et al. 1994).

Information analysis in this respect is based on the theory that the amount of information contained in a landscape determines the patterns displayed in the landscape and is a function of the information contained by each element within the landscape. Therefore, each element (or variable) contains a certain amount of information which contributes to the total information contained in the landscape. The total information is manifest in the landscape pattern. This information can be measured and the relative contribution of each element to the whole observed pattern can be determined.

Information in this sense refers to a measure of the knowledge gained when the amount of uncertainty or entropy contributed by the element is calculated. Maximum uncertainty equals maximum entropy. Theoretically, the mathematics of information theory lead to a maximum entropy approaching 1, as in equation 1:

$$H_{max}(A) = \ln m \text{ when } p_j = 1/m, \forall j \qquad (1)$$

when m represents the number of classes of a variable, j represents a particular class, and there is an equal probability of each class being sampled.

Entropy is minimized (ie. uncertainty is minimized) when the probability associated with one class is high while the other is low, as in

$$H_{min}(A) \approx 0 \text{ when } p_{*j} \approx 1 \text{ and } p_j \approx 0, \ \forall j \neq {*j} \qquad (2)$$

In other words, entropy is maximized when the amount of information contributed by any class is low and minimized when the amount of information contributed by any class is high.

In a practical two-state system (ie. presence or absence of tracks), however, the maximum entropy will lie somewhere between the extremes. This represents an amount of uncertainty, greater or lesser, that cannot be predicted as one element constrains the expression of another.

It is possible to understand the amount of information which each class contributes to the total entropy by calculating the mutual information relative to each class. This gives a measure of the uncertainty which is removed given a knowledge of the amount of information contributed to the whole by each class. The equation expressing this is given by

$$I(A,B) = H(A) - H_B(A,B) \tag{3}$$

where

$$H_B(A) = -\sum[p_i \times H_i \ (A)] \tag{4}$$

where H(A) represents the initial entropy of the system and H_B represents the entropy of the system given a knowledge of B.

Prior to the information analysis, the dataset was modified to be accepted by PEGASE, which operates only on discrete, categorical variables. A continuous variable, such as distance must be divided into discrete segments, for example, ten-metre intervals. The values of variables must be coded, for example, transect '2 west' becomes '22', habitat type 'mature conifer' becomes '3', as PEGASE accepts only numerical values.

Because PEGASE requires a matching number of 'non-observations' (ie. for each distance interval, there are equal probabilities of track presence or track absence), the original dataset used for the statistical analysis was expanded. The effective size of the dataset was doubled as additional 'non-observations' were added. The non-observations matched the observations proportionately with respect to distance interval and habitat type. In effect, the information analysis is based on the presence or absence of tracks in each ten-metre distance interval.

PEGASE operates by calculating the initial entropy of the whole dataset. The first division is then performed using the variable which provides the highest initial entropy. The second division uses the variable which provides the highest remaining initial entropy and so on, until stopping rules end the process. A defined level of significance, eg. $p = 0.05$, is a good stopping rule.

PEGASE also produces a dendrogram illustrating the relationships and the entropy contributed by each class of the variables. Each time a drop in entropy is encountered, it reveals the amount of uncertainty removed from the sample and indicates the relative contribution of the class to the observed pattern. Thus, one can clearly see which classes of the variables are most responsible for the observed pattern.

The mapped individual hare trails were examined in the context of the results of the statistical analyses to see if the patterns they showed echoed the statistical results. Similarly, trappers' knowledge was compared with the statistical results. The purpose of the trail maps and trappers' knowledge was to both illustrate the study's findings and offer 'real world' support.

3.5. Conclusion.

The study site was chosen to represent the variety of corridor-influenced habitats available in the disturbed landscape near Cochrane. The snow track survey method was chosen to take advantage of both well-defined tracks and easier movement in the bush in winter. Snow track surveys have been well-utilized by other researchers examining the spatial relationships of wildlife and habitat.

SAS offers a powerful tool for multivariate analysis, while information analysis offers another method of teasing out relationships and explaining them through the contribution of information to the whole observed pattern. Qualitative data such as observed animal behaviour, individual trails and trapper knowledge aid in interpreting the results of statistical and information analyses.

The following chapter presents the results of data analysis.

Chapter Four. Results.

4.1. Introduction.

This chapter presents the results of the research project, beginning with dataset descriptive statistics, followed by the multivariate analysis and ending with the information analysis. Hare results are presented separately from those of fox and lynx, because of their greater validity. Since the mapped hare trails and trappers knowledge are not statistical analyses, they will be presented briefly and discussed more fully in the next chapter.

The hare track sample was fairly large at 794 tracks, allowing for meaningful statistical analysis. The fox track sample was very small (n=30). The lynx track sample was even smaller (n=24). Therefore, very little can be said with any degree of certainty about either species.

However, as both species are predators with similar ranges, behaviours and prey preferences, it was decided to combine the two datasets and analyse the results together. The combined results for fox and lynx are called 'Predator' and will be presented together as preliminary results. The information analysis was not performed on the lynx and fox data because of the small sample size.

4.2. Results - Hare.

4.2.1. Descriptive Statistics - Hare.

Most hare tracks (n = 426 or 54%) were found in the second and third distance intervals corresponding to between 10 and 30 metres from the centre of the corridor (Figure 15, Table 1). More tracks than expected were found in the second (chi-square = 23.403, $p < 0.05$) and third distance intervals (chi-square = 13.893, $p < 0.05$). Fewer tracks (n=43 or 5%) than expected were found in the first distance interval corresponding to the corridor and its immediate edge (chi-square = 84.629, $p < 0.05$). Distance intervals 4 (30 to 40 metres) and 5 (40 to 50 metres) contained numbers of tracks close to expected values.

Most hare tracks (n=438 or 55%) were found in mature conifer habitat, with the next largest group (n=186 or 23%) being found in immature mixedwood (Figure 16, Table 1). Only 5% (n=43) were found in the corridor and its immediate edge. Mature hardwood

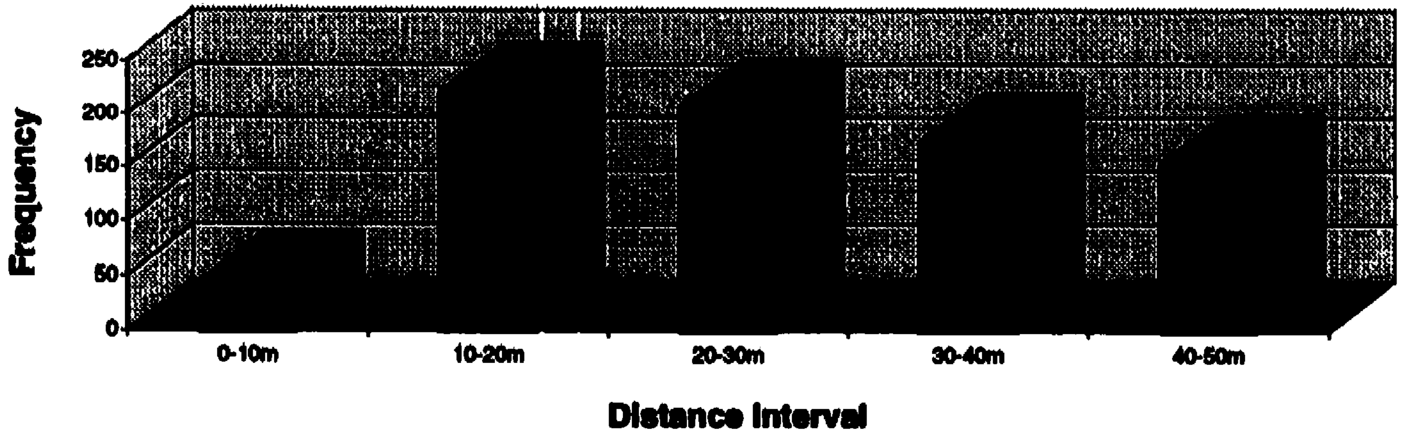


Figure 15. Graph of Distribution of Hare Tracks by Distance Interval.

Distance Interval	**Habitat Type**							**TOTAL**
	1 corridor & edge	**2** immature conifer	**3** mature conifer	**4** immature hardwood	**5** mature hardwood	**6** immature mixedwood	**7** mature mixedwood	
1 (0-10m)	43	0	0	0	0	0	0	**43**
2 (10-20m)	0	0	7	39	5	151	18	**220**
3 (20-30m)	0	0	168	0	11	14	13	**206**
4 (30-40m)	0	6	150	4	1	7	5	**173**
5 (40-50m)	0	20	113	1	1	14	3	**152**
TOTAL	**43**	**26**	**438**	**44**	**18**	**186**	**39**	**794**

Table 1. Contingency Table of Hare Data

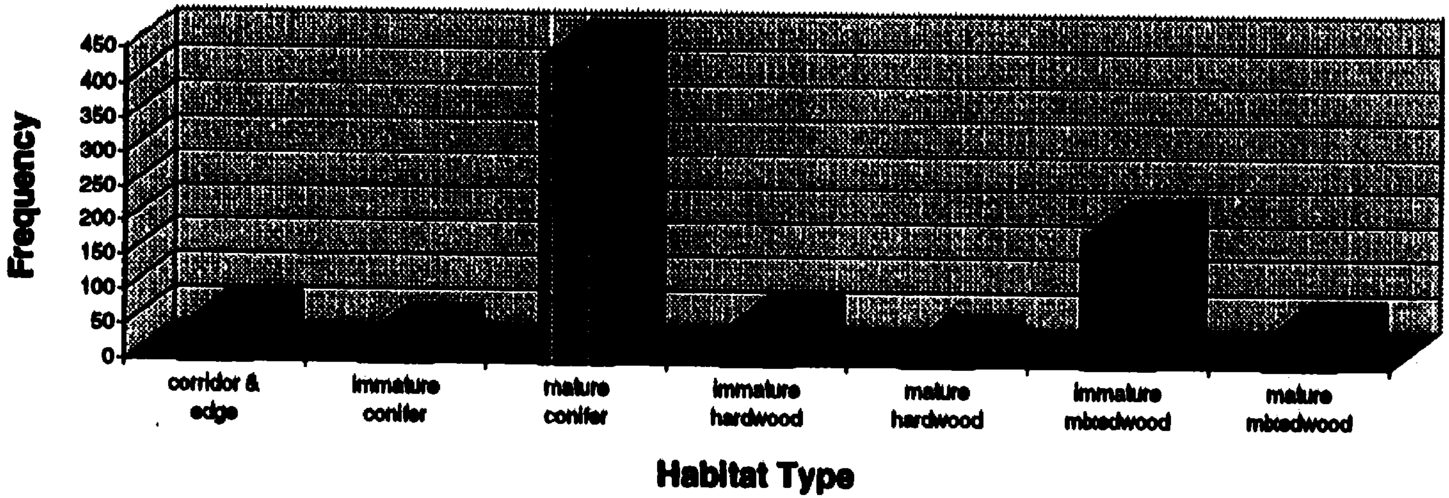


Figure 16. Graph of Distribution of Hare Tracks by Habitat Type.

contained the least number of hare tracks (n=18 or 2%). More tracks than expected were found in mature conifer habitat (chi-square = 118.229, $p < 0.05$). Less tracks than expected were found in corridor habitat (chi-square = 84.629, $p < 0.05$), immature conifer (chi-square = 16.071, $p < 0.05$), mature hardwood (chi-square = 6.125, $p < 0.05$) and mature mixedwood (chi-square = 20.253, $p < 0.05$). Immature hardwood and immature mixedwood habitat contained track frequencies close to expected values.

4.2.2. Multivariate Analysis - Hare.

The Shapiro-Wilk test yielded a value $W = 0.908383$, $p < W = 0.0$, for the whole hare dataset. Variance $s^2 = 2.047$, skewness = 0.56867 and kurtosis = 0.1625 for the dataset. This indicates a normal but positively skewed distribution. Each contributing transect was also tested. Most transects were normally distributed, but with differences in variances ranging from 0.00 to 4.25, skewness ranging from -0.00594 to 2.236068 and kurtosis ranging from -0.06239 to 5.00000, with some transects showing platykurtic distributions and some showing leptokurtic distributions. Thus, with tendencies to kurtosis, small sample sizes and apparent heterogeneity of variances, nonparametric statistical tests seem to be indicated.

A test of homogeneity was performed to justify lumping transects for further analysis. The Kruskal-Wallis analysis of variance by ranks yielded $H = 17.55$, $0.5 < p < 0.9$, not significant. It is therefore appropriate to pool transects for statistical analysis.

Likelihood-ratio testing yielded a G value of 613.707, p = 0.000, indicating that the variables Distance and Habitat are not independent and that tracks are clumped.

The loglinear analysis yielded the following results:

Variable	Chi-square	DF	Prob
Distance	388.79	7	0.0000
Habitat	15.66	5	0.0079
Distance*Habitat	229.56	18	0.0000

This indicates that distance influences track distribution more than habitat, with a strong distance/habitat interaction influencing track distribution as well. These results point to the conclusion that certain distance/habitat combinations are responsible for much of the observed track pattern. The information analysis described below aids in determining these specific combinations.

The correlation analysis resulted in a Spearman correlation coefficient of -0.645, p = 0.026, indicating a significant correlation between distance and habitat. This correlation also necessitates nonparametric analysis.

4.2.3. Information Analysis - Hare.

The nonparametric information analysis was used to analyse the correlated variables, as information analysis is free from the effects of correlation and non-independence of variables. The results of the information analysis are found in Appendix 1 and summarized in pictorial form in Figure 17. The results indicate that Distance contributes more to the observed track pattern than does Habitat as shown by a greater contribution to the negentropy of the dataset (54.1% versus 45.9%).

Specific combinations of variable classes contribute much to the track pattern. Corridor/0 to 10 metres, corridor/10 to 20 metres, mature conifer/10 to 20 metres, immature hardwood at all distance intervals, mature hardwood/10 to 20 metres, mature hardwood/20 to 30 metres, mature hardwood/40 to 50 metres and mature mixedwood at 20 to 30, 30 to 40 and 40 to 50 metres are all combinations showing the greatest contributions to the entropy of the dataset. These represent the combinations of variable classes that contribute the most to the observed track

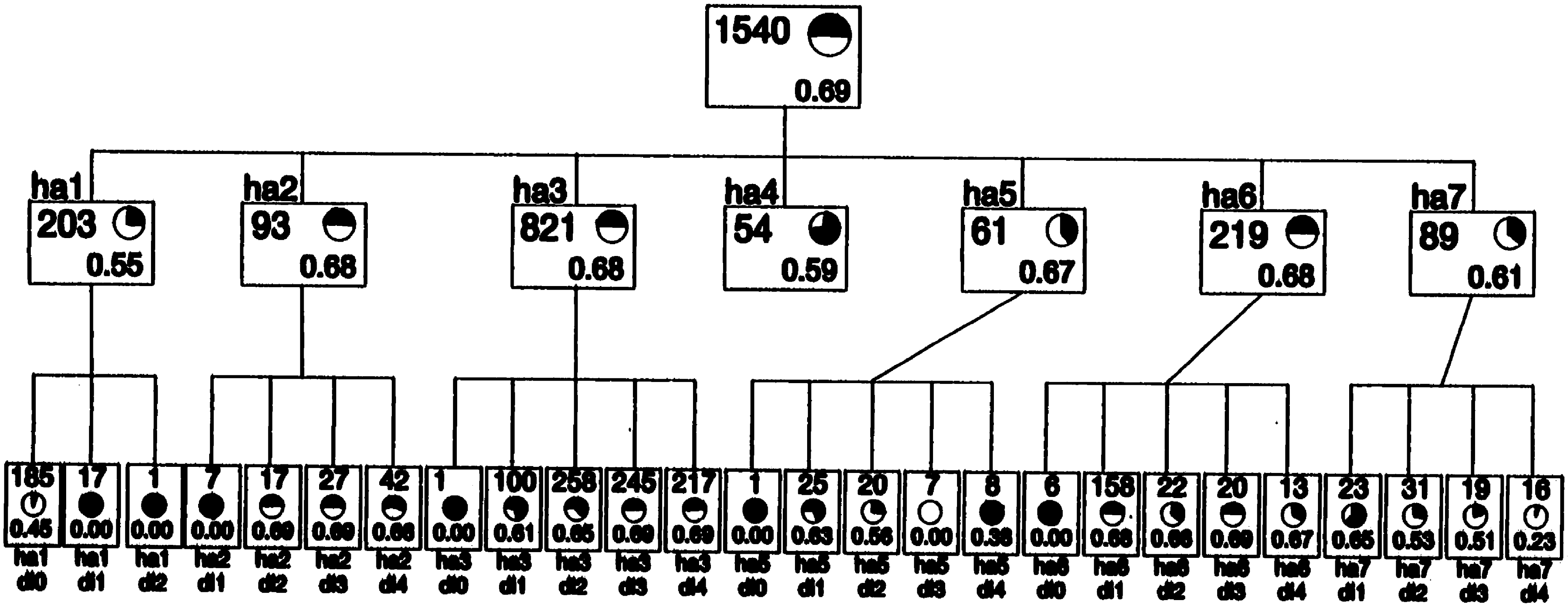


Figure 17. Dendrogram of Information Analysis.

pattern and are presented in Table 2. Table 3 shows the change in entropy at each division.

However, the total redundancy of the dataset is only 12%, indicating that the variables Distance and Habitat contribute only a small part to the observed track pattern. Other variables not sampled probably contribute the bulk of the information contained in the track pattern.

Combination	**Final Entropy** (from initial entropy = 0.69)	**Track Frequency/Total**
ha1/di0	0.45	31/185
ha3/di1	0.61	70/100
ha5/di1	0.63	17/25
ha5/di2	0.56	5/20
ha5/di4	0.38	1/8
ha7/di2	0.53	7/31
ha7/di3	0.51	4/19
ha7/di4	0.23	1/16

Table 2. Table of Selected Habitat/Distance Combinations.

Division	**Number of Subsets**	**Initial Entropy**	**H(E)**
0	1	0.693	0.000
1	7	0.655	1.459
2	9	0.637	1.501
3	12	0.634	1.575
4	16	0.628	2.290
5	20	0.621	2.342
6	24	0.617	2.477
7	27	0.611	2.556

Table 3. Table of Change of Entropy at Each Division of Information Analysis.

4.2.4. Individual Trails - Hare

The ten individually-mapped hare trails are illustrated in Appendix 2. Obvious in most trail diagrams is the tendency of hare to parallel the corridor, slightly inside the forest's edge, before crossing. Crossings are usually at right angles to the corridor. The diagrams show an increased tendency to 'zigzag' in the area near the corridor, as opposed to generally linear travel in the bush.

4.3. Results - Fox and Lynx.

As stated earlier, the fox and lynx sample sizes were small and therefore were analysed both separately and together. The results are given below to suggest possible trends to be investigated later with a larger sample.

4.3.1. Descriptive Statistics - Fox and Lynx.

The greatest number of fox tracks (n=10 or 30%) were found 40 - 50 metres from the centre of the corridors, with only three tracks (9%) found in the first distance interval, 0 - 10 metres from the centre of the corridors (Figure 18, Table 4). Goodness-of-fit testing did not reject the hypothesis that fox use distance intervals in proportion to their availability (chi-square = 7.5, $p > 0.05$, not significant).

Slightly less than half of all fox tracks (n=14 or 47%) were found in mature conifer with 40% (n=12) being found in immature mixedwood habitat (Figure 19, Table 4). The remaining four tracks were found in the corridor and in immature conifer. The hypothesis that fox used habitat types in proportion to their availability was not rejected at $p < 0.05$ (chi-square = 6.25, $p > 0.05$, not significant (25% expected frequencies < 5)). However,

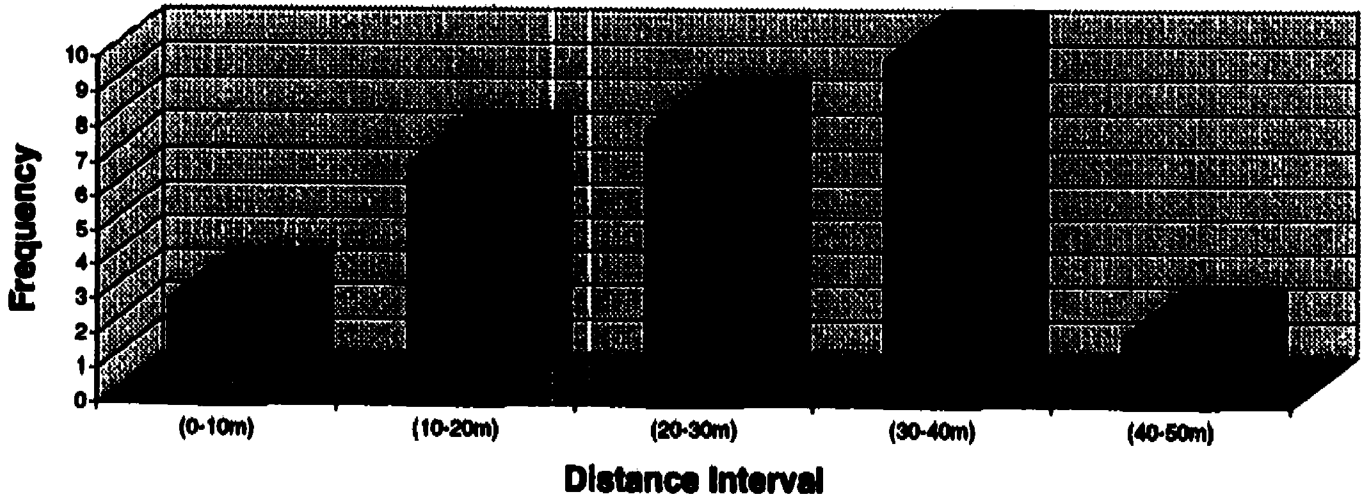


Figure 18. Graph of Distribution of Fox Tracks by Distance Interval.

Distance Interval	**Habitat Type**							**TOTAL**
	1 corridor & edge	**2** immature conifer	**3** mature conifer	**4** immature hardwood	**5** mature hardwood	**6** immature mixedwood	**7** mature mixedwood	
1 (0-10m)	3	0	0	0	0	0	0	**3**
2 (10-20m)	0	0	0	0	0	7	0	**7**
3 (20-30m)	0	0	6	0	0	2	0	**8**
4 (30-40m)	0	1	6	0	0	3	0	**10**
5 (40-50m)	0	0	2	0	0	0	0	**2**
TOTAL	**3**	**1**	**14**	**0**	**0**	**12**	**0**	**30**

Table 4. Contingency Table of Fox Data

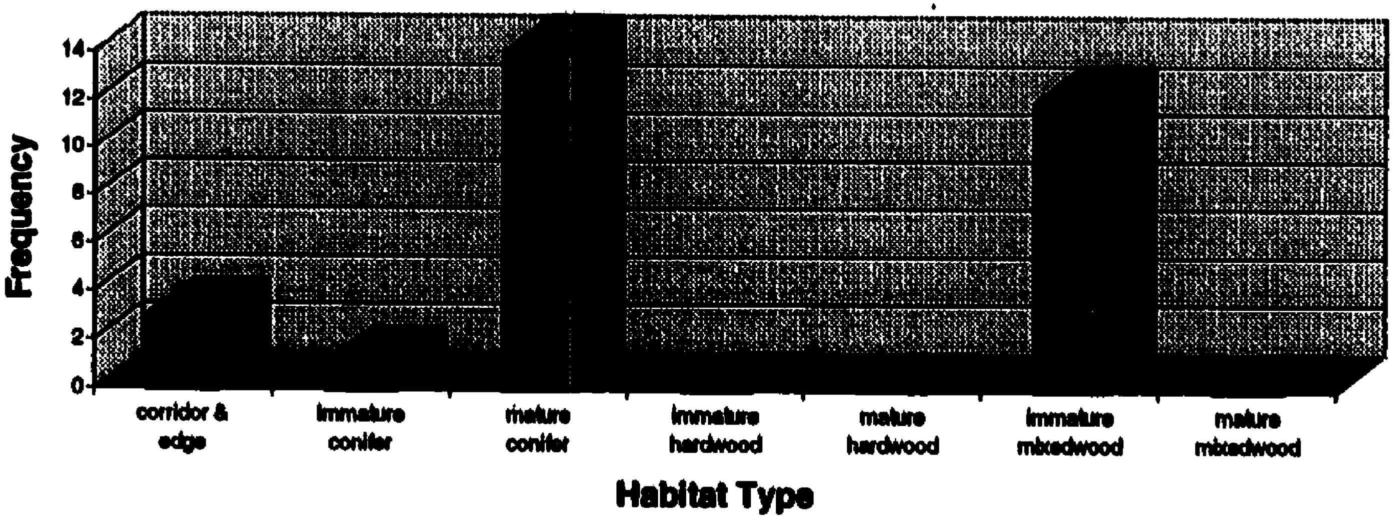


Figure 19. Graph of Distribution of Fox Tracks by Habitat Type.

at $p < 0.1$, analysis showed that fox tracks were not found in habitat types according to availability. Less fox tracks were found in hardwood habitat than expected.

More than half of all lynx tracks (n=14 or 58%) were found 20 - 40 metres from the centre of the corridors (Figure 20, Table 5). The rest (n=10 or 42%) were divided fairly evenly among the remaining distance intervals. Only three tracks (13%) were found in the 0-10 metre interval corresponding to the corridor and its adjacent edge habitat. The hypothesis that lynx tracks were found in each distance interval in proportion to its availability was not rejected (chi-square = 3.8, $p > 0.05$, not significant).

Half of all lynx tracks (n=12 or 50%) were found in mature conifer (Figure 21, Table 5). The remaining 12 lynx tracks were scattered evenly (n=3 or 13% each) throughout the rest of the habitat types, with the exception of no tracks found in immature hardwood and immature conifer. Goodness-of-fit testing indicated, however, that the hypothesis that lynx use each habitat type in proportion to its availability was not rejected (chi-square = 1.8, $p > 0.05$, not significant (25% expected frequencies < 5)).

The non-significance of the goodness-of-fit testing for fox and lynx separately may be due to the small sample sizes.

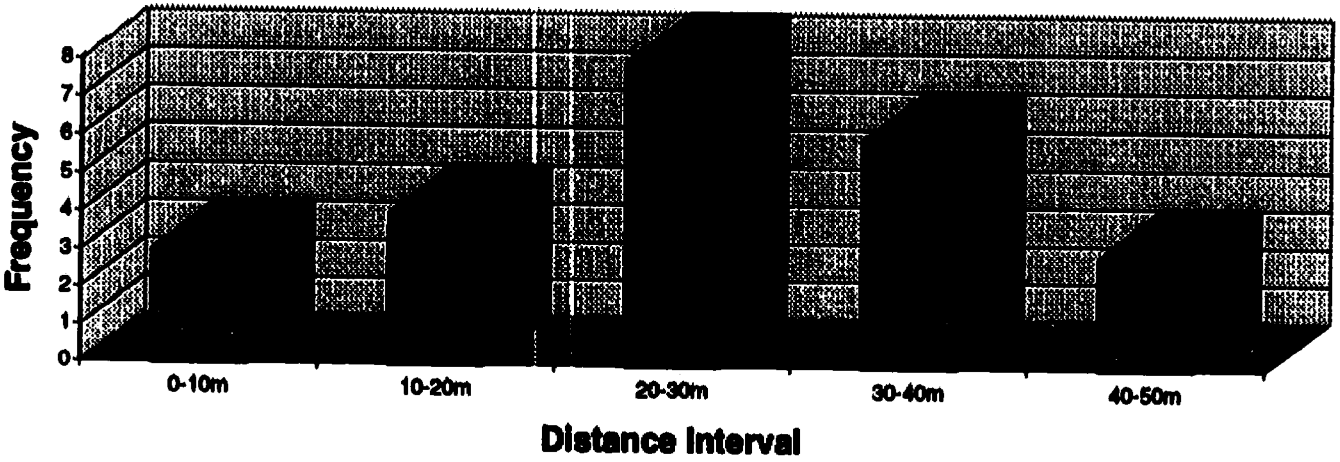


Figure 20. Graph of Distribution of Lynx Tracks by Distance Interval.

Distance Interval	**Habitat Type**							**TOTAL**
	1 corridor & edge	**2** immature conifer	**3** mature conifer	**4** immature hardwood	**5** mature hardwood	**6** immature mixedwood	**7** mature mixedwood	
1 (0-10m)	3	0	0	0	0	0	0	**3**
2 (10-20m)	0	0	0	0	0	3	1	**4**
3 (20-30m)	0	0	5	0	3	0	0	**8**
4 (30-40m)	0	0	6	0	0	0	0	**6**
5 (40-50m)	0	0	1	0	0	0	2	**3**
TOTAL	**3**	**0**	**12**	**0**	**3**	**3**	**3**	**24**

Table 5. Contingency Table of Lynx Data.

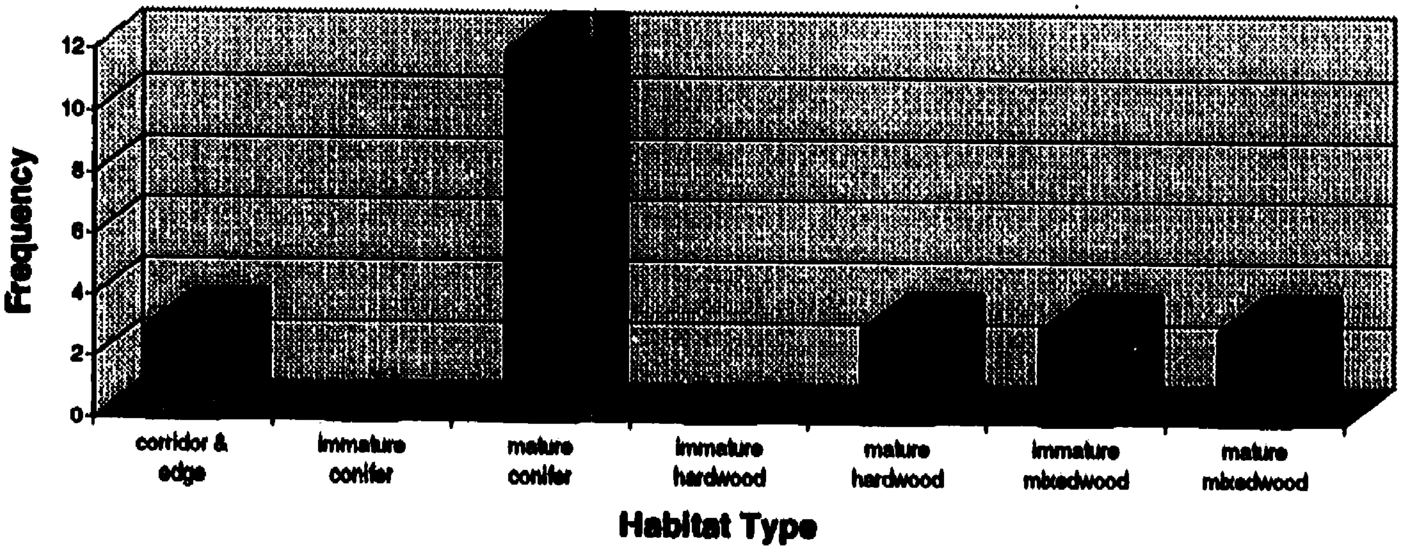


Figure 21. Graph of Distribution of Lynx Tracks by Habitat Type

When the datasets were combined into a 'predator' dataset (Table 6), goodness-of-fit testing indicated that distance intervals and habitat types are not used in proportion to their availability (distance: chi-square = 10.09, $p < 0.05$, significant; habitat: chi-square = 11.31, $p < 0.05$, significant). However, no variable class showed significant values at the $p < 0.05$ level, leading one to believe that a larger sample size may show significant variable class use. At the $p < 0.1$ level, analysis showed that predator tracks were found in mature conifer in greater than expected values (chi-square = 3.55). As well, they were found in distance interval 40 - 50 metres in less than expected values (chi-square = 3.27).

Goodness-of-fit testing was not able to reject the hypothesis that the track distribution of fox does not differ significantly from that of hare (distance: chi-square = 4.5704, $p > 0.05$; habitat: chi-square = 1.5, $p > 0.05$), although the small sample size may mask any trends actually present in the population. Likewise, the hypothesis that the track distribution of lynx echoes that of hare was not rejected (distance: chi-square = 6.9624, $p > 0.05$; habitat: chi-square = 0, $p = 1$). Similarly, the hypothesis that the combined fox and lynx track distribution echoes that of hare was not rejected (distance: chi-square = 8.1857, $p > 0.05$; habitat: chi-square = 1.6929,

Distance Interval	**Habitat Type**							**TOTAL**
	1 corridor & edge	**2** immature conifer	**3** mature conifer	**4** immature hardwood	**5** mature hardwood	**6** immature mixedwood	**7** mature mixedwood	
1 (0-10m)	6	0	0	0	0	0	0	**6**
2 (10-20m)	0	0	0	0	0	10	1	**11**
3 (20-30m)	0	0	11	0	3	2	0	**16**
4 (30-40m)	0	1	12	0	0	3	0	**16**
5 (40-50m)	0	0	3	0	0	0	2	**5**
TOTAL	**6**	**1**	**26**	**0**	**3**	**15**	**3**	**54**

Table 6. Table of Predator Data.

p > 0.05). Neither was the hypothesis that the track distributions of lynx and fox echo each other significantly rejected (distance: chi-square = 2.95, p > 0.05; habitat: chi-square = 1.5294, p > 0.05).

4.3.2. Multivariate Analysis - Fox and Lynx.

For fox, the likelihood-ratio test yielded a value of 36.993, p = 0.000. For lynx, the likelihood-ratio test resulted in a value of 47.639, p = 0.000. The significant values for both species indicate that distance and habitat are not independent of each other and that the track distribution is not random; rather, it is clumped.

Loglinear analysis yielded the following:

For Fox:

Variable	Chi-square	DF	Prob.
Distance	6	5	0.3068
Habitat	3	2	0.2067
Distance*Habitat	0	1	0.7074

For Lynx:

Variable	Chi-square	DF	Prob.
Distance	8	6	0.2764
Habitat	2	4	0.7880
Distance*Habitat	.	0	.

These non-significant results indicate that the hypothesis of no effect of distance or habitat on either species was not rejected.

Correlation analysis yielded a Spearman correlation coefficient of -0.082, p = 0.244, for fox and 0.175, p = 0.281 for lynx, indicating that the hypothesis that the variables are not significantly correlated was not rejected.

Likelihood-ratio testing on the pooled predator dataset yielded a value of 14.402, p = 0.002, indicating that the variables are not independent of each other and the track distribution is clumped. The Spearman correlation value was -0.080, p = 0.133, indicating that the hypothesis of non-correlation of variables was not rejected. The loglinear analysis on the pooled data gave non-signicant values as well (distance: chi-square = 0.10, p = 0.7515; habitat: chi-square = 7.80, p = 0.0503). Therefore, the hypothesis of no interaction of variables was not rejected.

4.4. Trappers Knowledge

Several trappers were informally questioned regarding their understanding of hare, fox and lynx behaviour and habitat preferences. As well, the trappers were asked where they trapped fox and lynx.

Trappers agree that hare cycles appear to influence both the abundance and distribution of fox and lynx. Fox are generally found in all habitat types and often use corridors to their advantage as travel routes through their ranges. Lynx are seldom seen and rarely use corridors. Instead, they are usually found in mature dense conifer.

4.5. Conclusion.

The analysis of the hare data yielded meaningful results, namely that distance and habitat both have an effect on the location of tracks, with distance showing a greater effect. As well, certain distance/habitat combinations contributed the most to the track pattern.

The fox and lynx analysis is more limited, as the sample sizes for each species were small. However, analysing the two datasets together yielded more meaningful results, namely that fox and lynx tracks are not found in habitat types or distance intervals in proportion to their availability. However, non-significant individual chi-square values do not shed much light on which habitat types or distance intervals are responsible. A larger sample is needed to answer this question.

The following chapter discusses the results, compares them to the literature, the mapped hare trails and trappers knowledge, and examines some non-scientific conjectures relating to them.

Chapter Five. Discussion.

5.1. Introduction.

The previous chapter's results indicate a clear relationship between the location of snowshoe hare tracks and both the distance from corridors and the habitat types in the landscape. However, no such firm conclusions, beyond the fact that analysis of the pooled predator dataset shows that tracks are not distributed according to distance and habitat availability, can be drawn for fox and lynx, probably due to the small sample size.

This chapter examines the results of the research in the context of the landscape and also in relation to others' work. It is important to emphasize again that the sample size for fox and lynx is very small, so that any generalizations offered must be treated as conjecture supported by personal observation and fitted in the context of other research.

5.2. Hare.

5.2.1. Hare - Descriptive Analysis.

Hare tracks were found significantly less than expected in corridor, immature conifer, mature hardwood and mature mixedwood habitat, while being found more than expected in mature conifer habitat. This indicates the importance of mature conifer as cover. However, the corresponding importance of habitat types containing suitable browse is not clearly indicated. Instead, hare tracks are found in immature hardwood and immature mixedwood habitat in proportion to availability.

Most of the hare tracks were concentrated 10 - 30 metres from the centre of the corridor. This indicates a concentration of activity close to, but not in, the corridor. Rather, the tracks are clumped several metres within the forest. If hare were indifferent to corridors, one would expect to see more tracks within the corridor and deeper within the forest, rather than concentrated in a relatively thin band between the two. The habitat near the corridor is usually qualitatively different from that within the interior of the forest (eg. more hardwoods and younger age classes). Yet even in transects where the habitat is uniform throughout, hare tracks are concentrated slightly in from the corridor.

This would seem to indicate a possible counteracting attraction/repulsion effect of the corridor. The following sections examine this possibility, with statistical analysis confirming that hare tracks are not located randomly with respect to either distance from the corridor or habitat type and information analysis revealing that distance from the corridor is more important to determining track location than habitat type.

5.2.2. Hare - Statistical Analysis.

For the hare data, likelihood ratio testing rejected the null hypothesis of random distribution of hare tracks with respect to distance from the centre of the corridors and habitat type ($G = 613.707$, $p = 0.000$). Loglinear analysis was also performed. Loglinear analysis fits the best model to the contingency table and compares its distribution to a chi-squared distribution (Zar 1984). Once the best-fit model was fitted to the hare data, the chi-square value became 388.79 (DF = 7, p = 0.000) for distance, 15.66 (DF = 5, p = 0.0079) for habitat and 229.56 (DF = 18, p = 0.000) for the distance/habitat interaction, confirming the rejection of the null hypothesis of independence.

The results of the loglinear analysis also indicate that there is indeed a distance effect. The habitat effect is much less. The habitat effect is still significant, but certainly much less so than the distance effect, indicating that habitat has far less influence on the distribution of hare tracks than does distance from the corridor. There is also a significant distance/habitat interaction. In other words, there is a link between the type of habitat that exists along the transect and the distance from the centre of the corridor in relation to the location of tracks.

The correlation analysis shows that there exists a negative relationship between distance and habitat in relation to the distribution of hare tracks (Spearman Correlation Coefficient = -0.645, p = 0.026). In other words, distance's influence on track distribution weakens further from the corridor, while habitat's influence increases further from the corridor. This indicates that the distance effect produced by the corridor is more significant to track distribution than is habitat effect, within a certain critical distance of the corridor (ie. 'edge effect').

5.2.3. Hare - Information Analysis.

The results of the information analysis indicate that the variable Distance contributes more to the negentropy of the dataset than does the variable Habitat (54.1% versus 45.9%). [Negentropy refers to the amount of uncertainty removed from the system and is analogous to the mutual information discussed earlier in Chapter Three (Phipps 1981a)]. This confirms the existence of a distance effect, superior to a habitat effect, with respect to the location of tracks.

However, it should be explained that the initial contribution of the variable Habitat to the negentropy of the system was greater (0.04) than that of the Distance variable (0.03) because at the first division Habitat contributed the most negentropy. Over the course of subsequent divisions, the total contribution of Distance to the negentropy of the system exceeded that of Habitat. In addition, it should be noted that the combined effect of distance and habitat resulted in a higher contribution to the negentropy (0.04) than did distance alone (0.03), illustrating the importance of the distance/habitat interaction.

The redundancy of the dataset is given as 12% for the 27 terminal subsets and is considered significant since the redundancy measured at each division is significant. Redundancy refers to the proportion of initial entropy which is removed by the divisive variable and is given by

$$R_B(A) = I(A,B)/H(A) = [H(A) - H_B(A)]/H(A) \qquad (5)$$

where I(A,B) represents the mutual information calculated between variables A and B, while H(A) is the initial entropy of the system. A relatively low redundancy of 12% indicates that a combination of variables other than distance and habitat contributes the bulk of the information contained in the observed track patterns. In other words, the locations of hare tracks are also influenced greatly by factors other than habitat type and distance from corridors, for example, predator avoidance, snow depth, social behaviour, etc.

A closer examination of the characteristics of the information analysis' divisional subsets shows that specific combinations of variables provide relatively large amounts of information to the observed pattern. For example, in the first division, with habitat type as the divisive variable, it can be seen that only habitat types 1 (corridor and edge) and 4 (immature hardwood) contribute significantly to the reduction in entropy of the system (0.14 and 0.1 respectively). The dendrogram (Figure 17) illustrates these relationships in pictorial form. These two habitats would appear to be generally avoided by hare.

The final division resulted in 27 subsets yielding interesting results with respect to the amount of negentropy contributed by each combination of variables. Table 2 presents significant combinations as well as their contribution to the negentropy of the system.

It can be seen that the ha1/di0 combination is significant. This is not surprising since this combination is highly correlated. After all, habitat type 1 is the corridor and its associated edge vegetation, while di0 (0 to 10 metres) represents the distance interval which contains the corridor. The strong repulsion effect of the corridor is indicated by a low frequency of track observations compared to the total observations plus 'non-observations' (31/185).

The ha3/di1 combination is significant and represents the mature conifer which exists in some transects adjacent to the corridor and its edge vegetation. This provides excellent cover close to a good food source (ie. corridor edge). The attraction effect of this habitat close to the corridor is indicated by the high frequency of tracks compared to the total frequency (70/100).

The combinations ha5/di1, ha5/di2 and ha5/di4 also contribute significantly to the negentropy of the system. This habitat, mature hardwood, provides little in the way of cover or browse. Its undesirability to hare is shown in the low proportion of tracks to the total for each of the last two combinations ha5/di2 and ha5/di4 (5/20 and 1/8 respectively). Yet, the relatively high occurrence of tracks in the combination ha5/di1 (17/25) indicates a significant distance effect, that is, hare tracks are concentrated in this distance interval (10 to 19.9 metres) regardless of the habitat. Perhaps the distinctive edge vegetation along the corridor is more significant for hare than is cover.

The combinations ha7/di2, ha7/di3 and ha7/di4 indicate that the presence of mature mixedwood is significant to the calculation of negentropy regardless of the distance from the corridor. That this habitat is avoided by hare is indicated by the low frequencies of track observations compared to the total sample frequency (7/31, 4/19 and 1/16 respectively). The change in entropy at each division is shown in Table 3.

Hare tracks are concentrated in certain well-defined habitats over others. Mature conifer is much used, undoubtedly due to the cover offered. Hare are known to feed only at certain times of day and remain under cover the rest of the time.

Habitat along corridors offers optimal conditions for hare because of the close association between cover and browse habitat. Young aspen and dogwood are available for food and dense mature balsam fir and spruce for cover. Most hare tracks were found in mature conifer, leading one to wonder if most of the hare's time is spent within the conifer, where numerous deadfall spruce offer secure resting places.

5.2.4. Hare - Literature Comparison.

The hare results confirm those of Wolff (1980) who found that hare preferred a mix of habitat types that provide cover and browse. Specifically, dense black spruce was sought for shelter. However, Wolff states that hare also seek dense black spruce stands to feed on spruce, willow and alder. The hare in the present study did not appear to feed on spruce or alder at all, choosing only dogwood and aspen. However, during times of high populations, I have observed hare feeding on spruce, balsam fir and tamarack.

It would seem that aspen is a preferred food source, found in immature mixedwood stands. Yet, hare tracks were found in this habitat only in expected values, rather than greater than expected values. During times of high populations, less preferred species such as tamarack and spruce may be browsed. Alder swales are found primarily in areas of black spruce, corresponding to areas of poor drainage and deep organic soil, and would offer cover to hare. However, there was no evidence of hare either browsing on alder or using it as cover in the Cochrane study area. In fact, on occasions when hare encountered alder swales, they circled around their periphery rather than travelling through them.

MacCracken et al. (1988) confirm the use of spruce, alder and willow as browse by hare, although they too found that alder did not form a preferred forage species. However, Ferron et al. suggest that habitat structure is more important to hare use than is vegetation species composition, at least in summer, with mature conifer stands and stands without immature and shrubby hardwoods considered low-utilization areas. This would make sense, given the low occurrence of browse in these habitat types. In the present study, the mature conifer stands appeared to be preferred habitat for cover, with hare going elsewhere to feed.

Ferron et al. also suggested that ecotones were very important for hare, with these areas being considered high-utilization areas. In the Cochrane study, relatively few tracks were found in the interior of habitat patches, particulaly the corridor and mature conifer. Instead, tracks were concentrated on the edges of habitat patches, confirming Ferron et al.'s conclusions.

The Cochrane study was undertaken during a time of low hare population numbers. Therefore, Wolff's hypothesis that hare use only optimal habitat during population lows appears to be borne out by the results. Optimal habitat in this case combines mature dense black spruce with immature mixedwood stands containing young aspen in close proximity.

Keith et al. (1993) also suggest that dense willow, alder and regenerating aspen stands provide optimal habitat, but that patch size affects survivability of hare populations in fragmented habitat. Juvenile and adult dispersal becomes important to recolonizing these patches. In an area with numerous patches of feeding and cover habitat, recolonization would occur more easily. The Cochrane study location would appear to be such an area, with many different patch sizes and types.

An interesting aside concerns the feeding behaviour of hare. Several studies have noted the chemical defenses of boreal plants against herbivory (Bryant et al. 1989, Jogia et al. 1989, Rangen et al. 1994). Specifically, Swihart et al. (1994) have noted that snowshoe hare prefer twigs from mature aspen to those of young aspen. In the Cochrane study, it was noticed that immature aspen was frequently browsed upon but that mature fallen aspen provided an utopia for hare, with the snow around the deadfall intensely trampled and densely littered with fecal pellets.

This research project's results generally support those of Riewe (1979, 1980). He found that snowshoe hare avoided seismic line corridors except during times of high population pressure when they often fed upon the shrub vegetation at the edges of the lines. During other times, if hare crossed the seismic lines, they did so at right angles.

In the Cochrane study, it was found that hare rarely crossed the corridor, doing so at right angles. There was more sign of them feeding just within the bush at the edge of the corridor. Corridors clearly form a barrier to hare movement, yet at the same time, hare appear to be attracted to the distinctive edge habitat types accompanying many corridors.

5.2.5. Hare - Individual Trails.

The ten individually-mapped hare trails yielded some interesting illustrative information (Appendix 2). It cannot be considered 'scientific' in that the data was not statistically analysed. However, a close examination of the trails resulted in apparent 'patterns', which in turn generated a series of possible explanations which may be tested at a later date. As these explanations are both speculative and behavioural in nature, it is not intended that they be interpreted in any other than a preliminary, qualitative and possibility-stating manner. Their inclusion in this dissertation is meant to allow both the researcher and reader the opportunity to explore wide-ranging alternative explanations for the observed distribution of hare tracks.

In eight of the ten cases, the hare crossed the corridor at right angles. This represents the shortest route between forest edges. The diagrams do not show it, but the actual trails showed tracks widely spaced in a running pattern. This minimizes the time the animal stays in the open. In two instances (cases 6 and 9), the hare were also running, but crossed the corridor at an angle rather than perpendicular to it.

In all cases, the hare paralleled the corridor before entering it. Often they remained for a time just inside the alder at the edge of the corridor or just inside the forest. Sometimes they paralleled the corridor only for a few metres and sometimes for many metres, but none immediately entered the corridor without having paralleled it first. This seems to indicate either a repulsion effect of the corridor or an attraction effect. Or both.

The corridor represents an open area lacking cover. However, it is possible that something on the other side of the corridor attracted the hare enough to justify crossing this open expanse, albeit as quickly and as safely as possible. The paralleling of the corridor prior to entering it may reflect a hesitation on the part of the hare.

Once on the other side, hare tracks were generally spaced closer together, indicating a slower pace. Some continued deeper into the forest, but many again paralleled the corridor, well within the alder or just within the forest. The tracks did not parallel the corridor, after crossing it, for as long a distance as they did prior to crossing it. This may also indicate an attraction effect of the habitat adjacent to the corridor, perhaps because of its combination of cover and browse, while the corridor itself represents a repulsion effect due to its openness and lack of cover.

In some cases, particularly case 8, the hare trail seemed to indicate a clear target destination. The trail paralleled the corridor for a relatively short distance before crossing it at right angles and proceeding directly to a blowndown mature aspen. Numerous trails intersected at this point, with the snow around and beneath the aspen being trampled and densely littered with fecal pellets. The fallen aspen was clearly an important food source for the hare. [The only hare that I had seen during the course of data collection was located at this site, browsing on aspen buds.] The hare (whether it was the one I had seen or not) may have had a prior knowledge of this tree and went directly to it by the shortest route, even crossing the corridor. This raises the question of whether hare remember the features of the landscape in which they live and can navigate confidently about their range based at least partially on remembered features.

Similarly, case 10 shows a trail in which the hare paralleled the corridor for several metres before crossing it at a right angle and proceeding to a deadfall spruce. Since the spruce was not a food source, it can be presumed that the hare used it for cover. Because of the density of tracks, it is again possible that the hare also had a previous knowledge of this spot and travelled directly to it based on that knowledge.

The corridor seems to possess both an attraction and a repulsion effect for hare. The open corridor itself is clearly repulsive to hare, judging by their track trails. They cross it as quickly as possible and do not remain in it for any length of time. On the other hand, their trails remain near it, perhaps because of the distinctive edge habitat associated with the corridor, which often provides both browse and cover. It is also possible that the hesitation noted earlier, as hare parallel the corridor prior to and following crossing it, may result in the observed increased track density with browse and cover habitat having little to do with it.

The individual hare trails recorded underscore the trends uncovered by the statistical and information analysis of this project's data. Tracks were concentrated slightly inside the forest's edge, where forage was easily available. Hare tracks were rare within the corridor but tended to cluster in greatly increased numbers along its edges, just within cover. If they crossed the corridor, it was usually at right angles, with the trail often having paralleled the corridor for some distance before finally crossing it. Hare trails were not noted crossing the wide expanse of the hydroline corridor at all.

5.2.6. Hare - Conclusion.

The hare results indicate a clear distance effect of the corridor on the track distribution. The 'edge effect' distance for hare appears to be about 30 metres from the corridor. A habitat effect, less clear but significant, is also present. The interaction between distance and habitat is also very important.

Hare tracks are concentrated in mature conifer habitat (in greater than expected numbers), but closer to the corridor rather than farther from it. Hare tracks were also widely found in the immature mixedwood habitat (in expected numbers) abutting the corridors, leading one to surmise that hare remain in the cover offered by mature conifer but also utilize the browse offered by immature mixedwood closer to the corridor. An interpretive examination of the individual trails offers support to these conclusions.

5.3. Fox and Lynx.

Because of the small sample size, the statistical analysis of the fox and lynx data (both by individual species and by pooled 'predator' dataset) can only be discussed in light of suggesting possible relationships which need to be tested later with a larger sample. Comparisons with the literature are also discussed.

5.3.1. Fox and Lynx - Descriptive Analysis.

Goodness-of-fit testing indicated that the hypothesis that fox tracks were found in both distance intervals and habitat types in proportion to their availability was not rejected at the $p < 0.05$ level (distance: chi-square = 7.5, $p > 0.05$; habitat: chi-square = 6.25, $p > 0.05$ (25% expected freqencies < 5)). However, at the $p < 0.1$ level, it was found that fox tracks were not found in habitat types in proportion to their availability (chi-square = 6.25, df = 3). Hardwood habitat contained fox tracks in less than expected numbers (chi-square = 3.00).

The hypothesis that lynx use both distance intervals and habitat types in proportion to their availability was not rejected (distance: chi-square = 3.8, $p > 0.05$; habitat: chi-square = 1.8, $p > 0.05$ (25% expected frequencies < 5)).

The non-significance of the goodness-of-fit testing for fox and lynx separately may be due to the small sample sizes. When the datasets were combined into a 'predator' dataset, goodness-of-fit testing indicated that distance intervals and habitat types do not contain track numbers in proportion to their availability (distance: chi-square = 10.09, $p < 0.05$; habitat: chi-square = 11.31, $p < 0.05$). However, no individual variable class showed significant chi-square values at the $p < 0.05$ level, leading one to believe that a larger sample size may show significant variable class use. At the $p < 0.1$ level, analysis showed that the combined fox and lynx tracks were found in mature conifer habitat more than expected. As well, the predator tracks were found 40-50 metres from the centre of the corridor in less than expected values.

5.3.2. Fox - Statistical Analysis.

For fox, likelihood-ratio testing yielded a *G* value of 36.993, p = 0.000, indicating a rejection of the null hypothesis of independence of variables. This also demonstrates that the track distribution is not random; tracks are clumped. Therefore, fox track distribution may be influenced by an interaction between distance and habitat.

Yet, a loglinear analysis yielded a chi-square value of 6 (DF = 5, p = 0.3068) for distance, 3 (DF = 2, p = 0.2067) for habitat and 0.14 (DF = 1, p = 0.7074) for the distance/habitat interaction. Such values are not deemed significant.

As well, correlation analysis did not reject the hypothesis of no correlation between habitat and distance (Spearman Correlation Coefficient = -0.082, p = 0.244).

The inconsistencies of results from the three tests are probably due to the small sample size which diminishes the power of the tests to detect statistically significant differences.

5.3.3. Lynx - Statistical Analysis.

For lynx, rejection of the null hypothesis of independence of variables is indicated by a likelihood-ratio *G* value of 47.639, p = 0.000.

Yet, as for the fox data, the loglinear analysis provided non-significant chi-square values of 7.51 (DF = 6, p = 0.2764) for distance and 1.71 (DF = 4, p = 0.7880) for habitat and no values for the distance/habitat interaction.

As well, the correlation analysis did not reject the null hypothesis of no correlation between distance and habitat (Spearman Correlation Coefficient = 0.175, p = 0.281).

As with the fox data, the inconsistencies reflect a sample size which may be too small for these tests to detect significant differences. A larger sample size is indicated for each species.

5.3.4. Fox and Lynx - Pooled Analysis.

Analyzing the pooled fox and lynx data strengthens the analysis and offers a more secure foundation upon which to base further assertions.

Likelihood-ratio testing on the pooled dataset yielded a *G* value of 14.402, p = 0.002, indicating that the variables are not independent of each other and the track distribution is clumped. The Spearman correlation value was -0.080, p = 0.133, indicating that the hypothesis of non-correlation of variables was not rejected. The loglinear analysis on the pooled data gave non-signicant values as well (distance: chi-square = 0.10, p = 0.7515; habitat: chi-square = 7.80, p = 0.0503).

However, the lower (yet still non-significant) probabilities for the correlation and loglinear analysis indicate that a larger sample may capture more of the variation in the populations' track distributions and thus yield significant results.

5.3.5. Fox - Literature Comparison.

Distribution of the fox and lynx track data does allow for some preliminary interpretations and comparisons with the literature. Fox tracks were found primarily in mature conifer and immature mixedwood habitats, echoing the primary locations of hare tracks. No fox tracks were found in immature or mature hardwood or mature mixedwood habitats, also echoing the fact that few hare tracks were found in these habitat types.

The distribution of fox tracks confirms Thompson et al.'s (1989) report that fox prefer successional boreal mixedwood stands of 10 - 30 years old. Other studies (eg. Riewe 1979, 1980) also show fox as creatures of edge and ecotone habitat.

The distribution of fox tracks by distance interval appears to be slightly different from snowshoe hare, although goodness-of-fit testing does not capture this, probably due to the small fox sample size. Where the greatest frequency of hare tracks were found 10-20 metres from the centre of the corridor and decreased evenly thereafter, the frequency of fox tracks increased fairly evenly across distance intervals until peaking 30-40 metres from the centre of the corridors, giving an 'edge effect' distance of about 40 metres from the corridor.

Foxes are not as dependent upon hare as lynx are (Elton and Nicholson 1942, Brand and Keith 1979, White and Ralls 1993); therefore, this distribution may reflect other factors not considered in the study, such as distribution of alternate prey species, or the location of dens. As well, the small sample size could be indicating a biased distribution which would not be borne out with a larger sample size.

Fox tracks were also found in the corridors, often following snowmobile or snowshoe trails. Fox appear to use corridors as travel routes. One fox trail was observed for twelve kilometres along an abandoned winter trail. Casual observation of foxes trotting along the sides of gravel roads shows that their pace of travel neither increases nor slackens; they occasionally glance at vehicles sharing the road but do not flee them.

Indeed, foxes appear to be one of the species that may actually benefit from the existence of corridors. Corridors may offer a convenient way for them to travel. Foxes have even been observed denning in holes dug in the sides of ditches along roads, even well-travelled secondary highways. Riewe (1979, 1980) found that fox appeared indifferent to corridors as well. In his studies, they sometimes followed seismic line corridors for a certain distance, and sometimes they just crossed them. But they certainly did not avoid them.

Foxes may also prefer the habitat near corridors because of the concentration of hares generally found in the successional habitat along abandoned roads, trails and ditches. It is fairly well-known among northerners that few species are found in large pure stands of mature conifer in winter. Such stands may provide cover but if there is no food source nearby, they will not be heavily utilized. Thus, edge habitat contiguous to mature conifer seems to be important for species such as snowshoe hare, fox and lynx.

5.3.6. Lynx - Literature Comparison.

Most lynx tracks were found in mature conifer habitat, with smaller, even distributions of tracks among the other habitat types, with the exception of immature conifer where no tracks were found. This distribution does not bear out Thompson et al.'s (1989) conclusion that lynx avoid mature conifer habitat, tending instead to be found in stands of mixedwood successional habitat of about 20 years old. Parker et al. (1983 in Thompson et al. 1989) confirm Thompson et al.'s findings.

On the other hand, Murray et al. (1994) found that lynx in their study preferred open spruce habitat and used very closed spruce stands as well, and tended to avoid open habitat and shrub habitat. The lynx data confirms their conclusion. However, in the Cochrane area, lynx are also often found in successional mixedwood and conifer habitat of about 40 to 80 years old.

Because lynx prey primarily upon snowshoe hare, it was expected that similar proportions of tracks would be located in corresponding habitat types. However, although the tracks of both species were found most often in mature conifer, hare tracks were found primarily in only two habitat types (mature conifer and immature mixedwood) and were found in very low percentages in all other habitat types.

On the other hand, lynx tracks were concentrated in mature conifer but were also found evenly distributed at a much lower percentage in all but one of the other habitat types. This may reflect the theory that carnivorous species, such as fox and lynx, are less selective in their habitat choice than are herbivores, such as hare. Again, a larger sample would be necessary to separate preference from prevalence.

The difference among distance intervals was much more striking. Although hare tracks were found in highest numbers 10-20 metres from the centre of the corridor and decreased evenly in frequency from 20-50 metres, lynx tracks were found in greatest numbers 20-30 metres from the centre of the transect. This may indicate a stronger corridor effect on lynx than hare, ie. the corridor has a stronger repulsion effect on lynx. Lynx may remain in dense mature conifer cover most of the time and hunt closer to the corridor where hare are most concentrated. The 'edge effect' distance for lynx appears to be about 40 to 50 metres from the corridor. Wolves are known to prey upon lynx; this may influence where lynx tracks are located as well.

Very few lynx tracks were found on the corridor. None crossed the corridor. Instead, the lynx tracks found on the corridor occurred in the very middle and followed the corridor for a considerable distance, up to one kilometre. If there were snowmobile or snowshoe tracks on the corridor, the lynx tracks followed these, possibly because snowmobile or snowshoe tracks compacted the snow, resulting in easier footing.

The following anectodal evidence is provided to aid in interpreting the lynx data. I have seen four lynx in my lifetime. One was on a gravel-surfaced logging road near Marathon, Ontario. I was able to get within six feet of a large lynx. We remained facing each other quietly for several minutes before I finally decided that it was foolhardy to be so close to a wild animal for no good reason. During that time, the lynx sat calmly on its haunches, with its ears forward, just watching me and sniffing the air. My impression was that the lynx was unafraid, even a bit curious. It remained sitting and watching me even after I left to return to my truck. Finally, it stood and slowly walked to the edge of the bush where it turned and watched me once again.

The next lynx I observed were near Cochrane. Two lynx were travelling one after the other through a 20 year old poplar stand about ten metres into the bush. One of them was carrying a snowshoe hare. This serves to support the hypothesis that lynx sometimes hunt together. The lynx were aware of our presence, but did not even break their stride. They just took a quick glance at us and continued trotting on their way.

The most recent lynx I saw was huddled on the snowbank at the side of highway 11 near Kirkland Lake, Ontario. It appeared to want to cross the highway but was apparently cautious of the vehicular traffic. I did not stop, so I do not know how long it waited or if it were successful in crossing the highway.

These anecdotes serve to indicate that lynx appear to be aware of the existence of corridors. They make use of them as travel corridors or cross them to access other areas of their range. Corridors seem to have an effect on lynx movement through the landscape. On the one hand, the data and the literature would appear to indicate that lynx avoid corridors for the most part, remaining in mature conifer.

Yet on the other hand, lynx evidently use corridors as travel routes and do not react in an apparently fearful manner when confronted by humans. The specific effects of corridors on lynx are both unclear and paradoxical. The small sample size in this study is not capable of providing enough information to get a better picture of the relationship of lynx to corridors. The anectodal evidence presented underlines this lack.

5.4. Trapper Information.

Trappers have long understood the behavioural patterns and habitat needs of wildlife species. However, their experiential knowledge has often been overlooked. The results of this project tend to confirm the knowledge and experience of local Cochrane trappers.

Hare are found primarily in landscapes combining immature aspen with mature conifer cover. Edge areas with their distinctive alder, dogwood and immature aspen vegetation complex are prime foraging habitat but must be situated close to mature conifer cover. Hare do not like to be in the open and thus avoid corridors. When they do cross them, they travel quickly as indicated by widely-spaced tracks. They also tend to cross at right angles.

Fox curiosity and relative lack of fear are their own worst enemy, making them fairly easy to trap along corridors and trails. However, fox are quick to learn and once trap-bit, they become quite cautious except when low prey supply leads to hunger overcoming good sense. Fox movement through the landscape appears to be largely independent of landscape pattern although they often use corridors in travelling about their ranges.

Lynx are more difficult to trap than hare or fox and are to be found where there is dense mature conifer. They are generally not found at corridor or forest edges; instead, they tend to stay slightly inside mature conifer cover, venturing out to obtain food or to travel to other areas.

None of the species is usually found deep in dense conifer forest (eg. more than 100 metres from any edge).

5.5. Conclusion.

For the purposes of this research, transect length was adequate for all species, but particularly so for foxes. Transects were long enough to catch the sudden drop in frequency after forty metres from the centre of the corridors for foxes. For lynx, the drop is there, but may be more an artifact of the small sample size. For hare, there is a general decrease rather than a sharp drop, but fifty metres is plenty of length to catch this trend.

In any case, it does serve to indicate an edge effect of the corridor for each species. For fox, it appears to be up to forty metres from the centre of the corridors. For hare, the effect decreases fairly evenly from twenty to thirty metres from the centre of the corridor. For lynx, the edge effect is less pronounced after thirty metres and certainly after forty metres from the centre of the corridors. Slightly longer transects (eg. 75 to 100 metres) would perhaps better show the edge effect distance.

As well it is important that all transects be the same length. The reason that the hydroline transects were initially longer is because the corridor itself is much wider than the other corridors. Therefore, the transect was lengthened to adjust for this increased width. All other corridors were roughly the same width. It would be better, perhaps, to perform a separate analysis on the hydroline transects, if the sample size were larger, in order to eliminate the difference in results due to differing corridor widths.

Similarly, the bush control transect should be studied independently and a larger sample taken. This problem would have been eliminated as well if transects began at the edge of the bush instead of in the middle of the corridor. Unfortunately, then there would be no way of recording the relative lack of tracks on the corridor itself.

However, when observations from the hydroline and bush transects and those that exceeded the 49.9-metre mark were removed from the dataset, it was found that the curves of the distance and habitat graphs remained consistent although the frequencies altered slightly. Test values changed slightly but were still significant. For this analysis, then, the difference between datasets that include the hydroline transects and those that do not is not enough to alter the significance of the results.

The findings of this research project generally support those of other authors, with the exception of alder as a favourable browse species. Hare track distribution seems to be primarily determined by the distance from the corridor, with the interaction of distance and habitat as a secondary influence. The influence of habitat, per se. is much lower.

The following chapter concludes the dissertation with a summary of the research project, a discussion of its implications and some management recommendations and ideas for further research.

Chapter Six. Conclusion.

The purpose of this research project was to investigate the relation between the winter track patterns of snowshoe hare, lynx and fox and the landscape pattern of an anthropogenically-disturbed area consisting of open corridors within the forested matrix of northeastern Ontario. The study area was typified by a patchy matrix of successional forest overlain with linear corridors, ie. hydroline, abandoned highway and old ditch. A control area of successional forest and original conifer forest was also included in the study area.

Questions asked were related to how the locations of hare, fox and lynx tracks were influenced by distance from corridors and habitat type. What are the effects of corridors on hare, fox and lynx track distributions? Is there a distance effect? A habitat effect? Or an interaction of distance and habitat? Is one secondary to the other? How strong are these effects, if present? Can an 'edge effect' distance be determined for each species? How do the distributions of hare, lynx and fox tracks relate to each other? The answers to these questions have relevance to landscape management and resource management planning as well as for recreational users and trappers.

The questions were posed as the following hypotheses:

1. Snowshoe hare tracks are distributed randomly with respect to discrete habitat types located along transects.
2. Snowshoe hare tracks are distributed randomly with respect to distance along transects.
3. There is no difference in the distance and habitat effects on hare tracks.
4. There is no correlation between distance from the corridor and habitat type along transects in relation to hare tracks.
5. All distance/habitat combinations contribute equally to the observed hare track pattern.
6. Red fox tracks are distributed randomly with respect to discrete habitat types located along transects.
7. Red fox tracks are distributed randomly with respect to distance along transects.
8. There is no difference in the distance and habitat effects on fox tracks.
9. There is no correlation between distance from the corridor and habitat type along transects in relation to fox tracks.
10. All distance/habitat combinations contribute equally to the observed fox track pattern.
11. The distribution of fox tracks with respect to distance from corridor echoes that of hare.
12. The distribution of fox tracks with respect to habitat type echoes that of hare.

13. Lynx tracks are distributed randomly with respect to discrete habitat types located along transects.

14. Lynx tracks are distributed randomly with respect to distance along transects.

15. There is no difference in the distance and habitat effects on lynx tracks.

16. There is no correlation between distance from the corridor and habitat type along transects in relation to lynx tracks.

17. All distance/habitat combinations contribute equally to the observed lynx track pattern.

18. The distribution of lynx tracks with respect to distance from corridor echoes that of hare.

19. The distribution of lynx tracks with respect to habitat type echoes that of hare.

20. The distribution of lynx tracks with respect to distance echoes that of fox.

21. The distribution of lynx tracks with respect to habitat echoes that of fox.

The literature relating to hare, fox and lynx habitat requirements is fairly extensive, but sometimes contradictory. Habitat use in one part of the world often differs from the same species' habitat use somewhere else. This reinforces two ideas: firstly, the results of any study are limited only to that study area during that time period, and secondly, that animals are influenced by evolutionary processes as well, ie. they learn to adapt to what is available.

The literature relating specifically to hare, fox and lynx use of corridors is scanty and limited primarily to roads and hydrolines. The road information is generally backed up by scientific study; however, the hydroline information is largely conjecture and expert opinion. This study aimed to help fill this gap in the scientific literature.

The investigation was accomplished by using established snow track survey methods along permanently marked transects. Data was analyzed through goodness-of-fit and likelihood-ratio testing. Fitting the data to a loglinear model resulted in clearer results. These results were confirmed and refined through an information analysis using the PEGASE procedure. Illustrative information was derived from the researcher's experience, trapper information and the interpretation of individual hare trail maps.

Some problems associated with the winter track survey were noticed. Poor snow conditions (too soft/fluffy or too granular/icy) at the beginning and end of the winter meant poor snowshoeing (and several twisted ankles and knees!) as well as poor track retention. It seems best to confine a winter track survey in this area to January, February and March. This is contrary to Thompson et al.'s (1989) advice to do winter track surveys prior to mid-December in order to avoid complications due to overwinter mortality. As well, transects should be longer than 50 metres in order to clearly identify the edge effect of corridors on track distributions.

There were some cases of hare, fox and lynx following the snowshoe trails. This was occasional and, because the transects did not necessarily coincide with the snowshoe trails, should not have biased the results very much. The only way to mitigate this problem is to snowshoe transects only once. The removal of flagging tape from research sites is a perennial problem. A solution is to mark transects with paint.

The results of this project were interesting and a little surprising. Most hare tracks were found between 10 and 30 metres from the centre of the corridors. This shows that hare are moving slightly inside the forest, rather than at the edge itself. In fact, very few hare tracks were found in the corridor and along its immediate edge. The 'edge effect' distance for hare is within 30 metres from corridors.

Most hare tracks were found in mature conifer, which provides cover. The next largest group of tracks was found in immature mixedwood, providing browse and a small measure of cover. Mature hardwood, providing little browse and no cover, contained the least number of tracks. Goodness-of-fit testing showed hare use corridor, immature conifer, mature hardwood and mature mixedwood less often than expected, while using mature conifer more often than expected.

Statistical analysis confirmed that snowshoe hare tracks are not distributed randomly with respect to either distance from the corridor or habitat type, thus rejecting the null hypotheses # 1 and # 2. Loglinear analysis indicated a significant distance effect, superior to a habitat effect, with a strong distance/habitat interaction effect as well, thus rejecting the null hypothesis # 3. Correlation analysis uncovered a negative correlation between distance and habitat, thus rejecting the null hypothesis # 4.

The information analysis noted that the variable Distance Interval (ie. from the centre of the corridor) provided more information to the observed pattern than did the variable Habitat Type, confirming the results of the statistical analysis. This seems to indicate that the distance from the corridor, or edge effect, has a greater influence on the track patterns of hare than do the habitat types available in the area.

A significant distance/habitat interaction was noted, as indicated in several specific habitat/distance combinations, thus rejecting null hypothesis # 5. It is not clear from this research whether this result would change in areas lacking in suitable habitat or when the population is under stress. The information analysis revealed that certain combinations of distance and habitat contributed most to the observed track pattern.

The conclusions resulting from the study are that snowshoe hare avoid corridors, but that the edge habitat bordering the corridor provides hare with optimal feeding and cover habitat, if dense mature conifer is also present nearby. Hare appear to prefer remaining in mature conifer, venturing out to feeding areas occasionally. Cover seems to be more important to hare than browse, with proximity to cover greatly influencing their track patterns. Similar distributions among corridor types indicate a similar response to corridors regardless of their width.

These results largely confirm the literature, except that alder is not seen as a desired forage species by hare. The use and avoidance of certain types or ages of browse species were confirmed, with the previously-noted exception of alder. In particular, fallen mature aspen provided the best browse for hare. The tendency for hare to stay slightly in from the edge was a detail not noted by other studies.

Goodness-of-fit testing was not able to reject null hypothesis # 6 (except at the $p < 0.1$ level), that fox track distribution is random with respect to habitat types. Most fox tracks were found in mature conifer and immature mixedwood habitat, although goodness-of-fit testing did not reveal significant class use at the $p < 0.05$ level. At the $p < 0.1$ level, analysis showed that fox tracks were found in hardwood habitat in less than expected numbers.

Fox tracks were concentrated 10 to 40 metres from the centre of the corridors, slightly further away from the corridor than were the bulk of hare tracks, giving an effective 'edge effect' distance of 40 metres from corridors. Again, however, goodness-of-fit testing could not reject null hypothesis # 7, that fox track distribution is random with respect to distance from the centre of the corridor.

Loglinear analysis revealed that one cannot reject null hypothesis # 8, that there is no difference in the distance and habitat effects on fox track distribution. Similarly, the results of the correlation analysis do not allow the rejection of null hypothesis # 9, that there is no correlation between variables. As well, the small sample size precluded testing for significance of individual distance/habitat combinations, so that null hypothesis # 10 could not be tested.

Lynx were creatures of mature conifer with their tracks to be found mainly 20 to 40 metres from the centre of the corridors, with an 'edge effect' distance of about 40 to 50 metres from the corridor. Goodness-of-fit testing was not able to reject null hypotheses 13 and 14, that track distributions are random with respect to distance and habitat. Lynx track patterns mimicked those of their prey, hare, as did fox, thus not rejecting null hypotheses # 11, 12, 18 and 19. As well, lynx and fox track distributions echoed each other with respect to both distance and habitat, thus not rejecting null hypotheses # 20 and 21.

Loglinear analysis could not reject null hypothesis # 15, that there is no difference in distance and habitat effects on lynx track distribution. No correlation was demonstrated between the two variables, thus null hypothesis # 16 could not be rejected. Again, the small sample size did not allow testing of null hypothesis # 17, that all distance/habitat combinations contribute equally to the observed track pattern.

However, when the fox and lynx datasets were combined, goodness-of-fit testing was able to reject the null hypotheses of random distribution with regard to distance and habitat, although no individual variable classes showed significance at the $p < 0.05$ level. At the $p < 0.1$ level, analysis showed that the combined fox and lynx tracks were found in mature conifer in greater than expected numbers. As well, predator tracks were found in the distance interval 40-50 metres from the centre of the corridor in less than expected numbers. It seems reasonable to conclude that a larger sample of both species would yield more meaningful results.

For fox, corridors appear to be incidental features of the landscape, useful when travelling but otherwise worth ignoring. In this study, fox clearly are not discomfited by corridors. Indeed, they take advantage of their availability as travel routes. Fox certainly do not avoid corridors. This is the opposite result to Storm's (1976) study in which fox avoided corridors. This leads one to wonder whether the corridor itself is the attraction/repulsion or whether other landscape elements (eg. houses, traffic or adjacent forest type) have a determining effect on fox movement.

Lynx appear to use corridors very occasionally for travelling but otherwise remain in mature conifer habitat. This study confirms their use of habitat as stated in the literature. And yet, even after this research was completed and the data analysed, the researcher is left with a feeling of mystery regarding lynx and their movement. Perhaps because the sample size was so small, the results are subject to much interpretive question. A larger sample over a broader area would be necessary to sort out relationships more clearly.

Although this study upholds trappers' beliefs, it challenges some notions held by the general public. Many people believe that human alteration of the landscape is inherently bad for wildlife, ie. it results in lower population numbers and a greater stress on individuals. This research seems to indicate that for the three species concerned, the opposite is likely. Human-made corridors appear to provide additional habitat for hare, perhaps resulting in an increase in population size, thus benefiting fox and lynx. Corridors also provide travel routes which are much utilized by fox and, to a lesser extent, lynx.

Of course, the same apparent benefits enjoyed by these species may be seen as constraints to other, interior species, such as cougar and mature reproducing marten. This just provides another lesson in the importance of a landscape ecological approach to the study of nature. Single species management may have its benefits, but it must always be placed within the context of the landscape. Managing for fox and hare may mean creating corridors and edge habitat, but if marten also exist in the area then their need for large tracts of interior habitat must be considered as well.

The challenge is to create a landscape mosaic which meets the needs of as many species as is practicable within the constraints of space and availability, given an understanding of species' needs, environmental factors and the natural history of the landscape. Management goals and objectives, from an economic and social perspective, also influence landscape management.

For example, the area surrounding Cochrane is under intensive forest management. Some areas are into a second and even third rotation. Forest management plans from 1987 to 1994 generally followed the **Timber Management Guidelines for the Provision of Moose Habitat** (OMNR 1988). The guidelines advocated relatively small clearcuts (generally less than 260 ha), resulting in numerous small patches consisting of much edge. Indeed, a requirement of the plans was to maximize edge to area ratios. The prevailing wisdom was that managing for moose also covered the habitat requirements for about 70% of boreal species. This resulted in a patchwork landscape through much of the Cochrane area, though not much of an increase in moose (a species not historically native to the Cochrane area).

Beginning with the 1995 Timber Management Plans, planners were required to implement 'biodiversity conservation' measures. There were several options available to achieving this, but most involved both larger clearcuts and larger leave areas, including wider reserves around waterbodies and other features of local importance. The theory was that interior species such as cougar and marten would benefit in the future from larger leave areas and would benefit in the present from more spatially-concentrated logging.

This research seems to indicate that a combination of the two above approaches, ie. the 'moose guideline approach' and the 'biodiversity approach', would be both practicable and desirable in the Cochrane area and perhaps elsewhere in the boreal forest. Forest management planners should establish zones of 'protection'. Areas which are closer to towns and recreational areas, and thus not as likely to host as many interior species, should be managed 'intensively', ie. smaller cutblocks, smaller leave blocks, less silviculture. This would benefit moose (lower hunting mortality, more browse as well as leave blocks for cover). It would also benefit grouse, hare, fox and lynx and the trappers who depend upon them. In addition, it would alleviate some of the concern of people who frown upon large clearcuts.

More remote areas should be managed 'extensively', ie. larger cutblocks, larger leave blocks, more intensive silviculture. This would benefit interior species as it results in less fragmentation and enough interior habitat to maintain populations indefinitely if even proportions of age classes are left. It would also benefit the local logging industry as it concentrates their operations, resulting in less time and money spent on road building and maintenance as well as silviculture and log and equipment transportation.

Sensitive areas, such as conservation lands and protected habitat features (eg. bald eagle nests) could easily be subsumed within either an intensive or extensive approach.

In both approaches, care should be taken to maintain or enhance existing networks of riparian buffers as well as forested linkages to mature forest blocks. This favours dispersal throughout the landscape for both forest and edge species. Of course, these networks would deteriorate in time and alternate networks would need to be examined at the end of each planning cycle (20 years).

By using such an approach, a landscape is designed which attempts in a considered and critical manner to meet the needs of the wildlife and plant species which inhabit it as well as the people who use, live and work in it. Even the place of industry is well-considered.

This was a worthwhile project for me. Data collection was a pleasure. I learned much about statistics, statistical software, database design, database software and research design. The results confirmed some previously-held notions while rejecting others. Yet each answer only served to open the door to more questions. Why do lynx track patterns not overlap more with hare patterns, their main prey species? What is it about corridors that apparently repulse lynx? Why is there a peak of fox tracks at 30 to 40 metres from the centre of corridors, when there are so few hare there? Corridors in and of themselves do not seem to bother fox.

These questions seem worth pursuing, to me. Future research projects will hopefully help to clear up some of the mystery.

"...there are more things in heaven and earth, than are dreamt of in your philosophy." (Shakespeare, Hamlet)

```
!!! memoire ptr pval= 4668 x 1 bytes!!!
!!! memoire str solut= nig/10 140 bytes !!!
************************************************
 Step # 1 Sub-set # 1 of  1  Sub-set_id#1000
 No sites: 1540; Entropy: 0.69
  non  act
  770 770

 2 Distance
 i Cod Clas  Tot  H(i)  non  act
 0  0  di0  197  0.52  154  43
 1  1  di1  374  0.68  154  220
 2  2  di2  354  0.68  154  200
 3  3  di3  319  0.69  154  165
 4  4  di4  296  0.69  154  142
Mut.inf.=0.028  Kulb.= 84.9  S.Ratio= 8.95  Rel.inf.=0.017  Chi2=**

 3 Habitat
 i Cod Clas  Tot  H(i)  non  act
 0  1  ha1  203  0.55  154  49
 1  2  ha2   93  0.68   39  54
 2  3  ha3  821  0.68  339  482
 3  4  ha4   54  0.59   15  39
 4  5  ha5   61  0.67   37  24
 5  6  ha6  219  0.68  124  95
 6  7  ha7   89  0.61   62  27
Mut.inf.=0.038  Kulb.=116.3  S.Ratio= 9.24  Rel.inf.=0.026  Chi2=**

The divisive variable is # 3 Habitat
i Cod Clas  Tot  H(i)  non  act
0  1  ha1  203  0.55  154  49
                0.76 0.24
                0.52-0.52

1  2  ha2   93  0.68   39  54
                0.42 0.58
               -0.16 0.16

2  3  ha3  821  0.68  339  482
                0.41 0.59
               -0.17 0.17

3  4  ha4   54  0.59   15  39
                0.28 0.72
               -0.44 0.44

4  5  ha5   61  0.67   37  24
```

```
              0.61 0.39
              0.21-0.21

 5  6 ha6  219 0.68 124  95
              0.57 0.43
              0.13-0.13

 6  7 ha7   89 0.61  62  27
              0.70 0.30
              0.39-0.39

Mut.inf.=0.038  Kulb.=116.3  S.Ratio= 9.24  Rel.inf.=0.026  Chi2=**

**************************************************
 Step # 2 Sub-set # 1 of  7  Sub-set_id#1001000
 No sites:  203; Entropy: 0.55
  non  act
  154  49
Characteristics of this sub-set:
 ha1

 2 Distance
 i Cod Clas  Tot H(i) non act
 0  0 di0  185 0.45 154  31
 1  1 di1   17 0.00   0  17
 2  2 di2    1 0.00   0   1
Mut.inf.=0.141  Kulb.= 57.1  S.Ratio= 9.54  Rel.inf.=0.442  Chi2=**

 3 Habitat
 i Cod Clas  Tot H(i) non act
 0  1 ha1  203 0.55 154  49
 1  2 ha2   93 0.68   0   0
 2  3 ha3  821 0.68   0   0
 3  4 ha4   54 0.59   0   0
 4  5 ha5   61 0.67   0   0
 5  6 ha6  219 0.68   0   0
 6  7 ha7   89 0.61   0   0
Mut.inf.=0.000  Kulb.= 0.0  S.Ratio= 0.00  Rel.inf.=0.000  Chi2=**

The divisive variable is # 2 Distance
i Cod Clas  Tot H(i) non act
0  0 di0  185 0.45 154  31
             0.83 0.17
             0.10-0.31

1  1 di1   17 0.00   0  17
             0.00 1.00
            -1.00 3.14
```

```
 2  2 di2    1 0.00   0   1
              0.00 1.00
             -1.00 3.14

Mut.inf.=0.141  Kulb.= 57.1  S.Ratio= 9.54  Rel.inf.=0.442  Chi2=**

**************************************************
 Step #  2 Sub-set #  2 of   7  Sub-set_id#1002000
 No sites:    93; Entropy: 0.68
  non  act
   39   54
Characteristics of this sub-set:
 ha2

 2 Distance
 i Cod Clas   Tot  H(i)  non  act
 1   1 di1     7 0.00    0    7
 2   2 di2    17 0.69    8    9
 3   3 di3    27 0.69   15   12
 4   4 di4    42 0.66   16   26
Mut.inf.=0.054  Kulb.= 10.1  S.Ratio= 1.29  Rel.inf.=0.044  Chi2=*

 3 Habitat
 i Cod Clas   Tot  H(i)  non  act
 0   1 ha1   203 0.55    0    0
 1   2 ha2    93 0.68   39   54
 2   3 ha3   821 0.68    0    0
 3   4 ha4    54 0.59    0    0
 4   5 ha5    61 0.67    0    0
 5   6 ha6   219 0.68    0    0
 6   7 ha7    89 0.61    0    0
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio= 0.00  Rel.inf.=0.000  Chi2=**

 The divisive variable is # 2 Distance
 i Cod Clas   Tot  H(i)  non  act
 1   1 di1     7 0.00    0    7
              0.00 1.00
             -1.00 0.72

 2   2 di2    17 0.69    8    9
              0.47 0.53
              0.12-0.09

 3   3 di3    27 0.69   15   12
              0.56 0.44
              0.32-0.23
```

```
 4  4 di4   42 0.66  16  26
               0.38 0.62
              -0.09 0.07

Mut.inf.=0.054  Kulb.= 10.1  S.Ratio= 1.29  Rel.inf.=0.044  Chi2=*

************************************************
 Step # 2 Sub-set # 3 of  7  Sub-set_id#1003000
 No sites:  821;  Entropy:  0.68
  non  act
  339  482
Characteristics of this sub-set:
 ha3

 2 Distance
 i Cod Clas  Tot  H(i)  non  act
 0  0 di0     1  0.00    0    1
 1  1 di1   100  0.61   30   70
 2  2 di2   258  0.65   93  165
 3  3 di3   245  0.69  108  137
 4  4 di4   217  0.69  108  109
Mut.inf.=0.010  Kulb.= 16.6  S.Ratio= 1.75  Rel.inf.=0.008  Chi2=**

 3 Habitat
 i Cod Clas  Tot  H(i)  non  act
 0  1 ha1   203  0.55    0    0
 1  2 ha2    93  0.68    0    0
 2  3 ha3   821  0.68  339  482
 3  4 ha4    54  0.59    0    0
 4  5 ha5    61  0.67    0    0
 5  6 ha6   219  0.68    0    0
 6  7 ha7    89  0.61    0    0
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio= 0.00  Rel.inf.=0.000  Chi2=**

 The divisive variable is # 2 Distance
 i Cod Clas  Tot  H(i)  non  act
 0  0 di0     1  0.00   0   1
                 0.00 1.00
                -1.00 0.70

 1  1 di1   100  0.61  30  70
                 0.30 0.70
                -0.27 0.19

 2  2 di2   258  0.65  93 165
                 0.36 0.64
                -0.13 0.09
```

```
 3  3  di3  245 0.69 108 137
                 0.44 0.56
                 0.07-0.05

 4  4  di4  217 0.69 108 109
                 0.50 0.50
                 0.21-0.14

Mut.inf.=0.010 Kulb.= 16.6 S.Ratio= 1.75 Rel.inf.=0.008 Chi2=**

 2 Distance
 i Cod Clas  Tot  H(i)  non  act
 0  0  di0    4  0.00   0   4
 1  1  di1   44  0.64  15  29
 2  2  di2    5  0.00   0   5
 3  3  di3    1  0.00   0   1
Mut.inf.=0.068 Kulb.= 7.3 S.Ratio= 0.94 Rel.inf.=0.104 Chi2=

 3 Habitat
 i Cod Clas  Tot  H(i)  non  act
 0  1  ha1  203  0.55    0   0
 1  2  ha2   93  0.68   0   0
 2  3  ha3  821  0.68    0   0
 3  4  ha4   54  0.59  15  39
 4  5  ha5   61  0.67   0   0
 5  6  ha6  219  0.68    0   0
 6  7  ha7   89  0.61   0   0
Mut.inf.=0.000 Kulb.= 0.0 S.Ratio= 0.00 Rel.inf.=0.000 Chi2=**

**************************************************
 Step # 2 Sub-set # 4 of  7  Sub-set_id#1004000
 No sites:  54; Entropy: 0.59
  non  act
   15  39
 Sub-set's characteristics :
 ha4
 Terminal sub-set # 0

**************************************************
 Step # 2 Sub-set # 5 of  7  Sub-set_id#1005000
 No sites:  61; Entropy: 0.67
  non  act
   37  24
Characteristics of this sub-set:
 ha5

 2 Distance
 i Cod Clas  Tot  H(i)  non  act
```

```
 0  0 di0    1 0.00   0   1
 1  1 di1   25 0.63   8  17
 2  2 di2   20 0.56  15   5
 3  3 di3    7 0.00   7   0
 4  4 di4    8 0.38   7   1
Mut.inf.=0.180  Kulb.= 21.9  S.Ratio= 2.31  Rel.inf.=0.137  Chi2=**

 3 Habitat
 i Cod Clas   Tot  H(i)  non  act
 0  1  ha1   203  0.55   0   0
 1  2  ha2    93  0.68   0   0
 2  3  ha3   821  0.68   0   0
 3  4  ha4    54  0.59   0   0
 4  5  ha5    61  0.67  37  24
 5  6  ha6   219  0.68   0   0
 6  7  ha7    89  0.61   0   0
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio= 0.00  Rel.inf.=0.000  Chi2=**

 The divisive variable is # 2 Distance
 i Cod Clas   Tot  H(i)  non  act
 0  0 di0      1  0.00   0   1
                 0.00 1.00
                -1.00 1.54

 1  1 di1     25  0.63   8  17
                 0.32 0.68
                -0.47 0.73

 2  2 di2     20  0.56  15   5
                 0.75 0.25
                 0.24-0.36

 3  3 di3      7  0.00   7   0
                 1.00 0.00
                 0.65-1.00

 4  4 di4      8  0.38   7   1
                 0.88 0.12
                 0.44-0.68

Mut.inf.=0.180  Kulb.= 21.9  S.Ratio= 2.31  Rel.inf.=0.137  Chi2=**

**************************************************
 Step #  2 Sub-set #  6 of  7  Sub-set_id#1006000
 No sites:  219;  Entropy:  0.68
  non  act
  124   95
Characteristics of this sub-set:
```

```
ha6

2 Distance
i Cod Clas  Tot  H(i)  non  act
0  0  di0    6  0.00    0    6
1  1  di1  158  0.68   93   65
2  2  di2   22  0.66   14    8
3  3  di3   20  0.69    9   11
4  4  di4   13  0.67    8    5
Mut.inf.=0.027  Kulb.= 12.0  S.Ratio= 1.27  Rel.inf.=0.029  Chi2=*

3 Habitat
i Cod Clas  Tot  H(i)  non  act
0  1  ha1  203  0.55    0    0
1  2  ha2   93  0.68    0    0
2  3  ha3  821  0.68    0    0
3  4  ha4   54  0.59    0    0
4  5  ha5   61  0.67    0    0
5  6  ha6  219  0.68  124   95
6  7  ha7   89  0.61    0    0
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio= 0.00  Rel.inf.=0.000  Chi2=**

The divisive variable is # 2 Distance
i Cod Clas  Tot  H(i)  non  act
0  0  di0    6  0.00    0    6
                  0.00 1.00
                 -1.00 1.31

1  1  di1  158  0.68   93   65
                  0.59 0.41
                  0.04-0.05

2  2  di2   22  0.66   14    8
                  0.64 0.36
                  0.12-0.16

3  3  di3   20  0.69    9   11
                  0.45 0.55
                 -0.21 0.27

4  4  di4   13  0.67    8    5
                  0.62 0.38
                  0.09-0.11

Mut.inf.=0.027  Kulb.= 12.0  S.Ratio= 1.27  Rel.inf.=0.029  Chi2=*

****************************************************
Step #  2 Sub-set #  7 of   7  Sub-set_id#1007000
```

```
 No sites:   89; Entropy: 0.61
  non  act
   62  27
Characteristics of this sub-set:
 ha7

 2 Distance
 i Cod Clas  Tot  H(i)  non  act
 1  1 di1   23 0.65   8  15
 2  2 di2   31 0.53  24   7
 3  3 di3   19 0.51  15   4
 4  4 di4   16 0.23  15   1
Mut.inf.=0.109  Kulb.= 19.4  S.Ratio= 2.48  Rel.inf.=0.080  Chi2=**

 3 Habitat
 i Cod Clas  Tot  H(i)  non  act
 0  1 ha1  203 0.55   0   0
 1  2 ha2   93 0.68   0   0
 2  3 ha3  821 0.68   0   0
 3  4 ha4   54 0.59   0   0
 4  5 ha5   61 0.67   0   0
 5  6 ha6  219 0.68   0   0
 6  7 ha7   89 0.61  62  27
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio= 0.00  Rel.inf.=0.000  Chi2=**

 The divisive variable is # 2 Distance
 i Cod Clas  Tot  H(i)  non  act
 1  1 di1   23 0.65   8  15
                 0.35 0.65
                -0.50 1.15

 2  2 di2   31 0.53  24   7
                 0.77 0.23
                 0.11-0.26

 3  3 di3   19 0.51  15   4
                 0.79 0.21
                 0.13-0.31

 4  4 di4   16 0.23  15   1
                 0.94 0.06
                 0.35-0.79

Mut.inf.=0.109  Kulb.= 19.4  S.Ratio= 2.48  Rel.inf.=0.080  Chi2=**

 2 Distance
 i Cod Clas  Tot  H(i)  non  act
 1  1 di1   23 0.65   0   0
```

```
 2  2 di2   31 0.53   0   0
 3  3 di3   19 0.51   0   0
 4  4 di4   16 0.23   0   0
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio= 0.00  Rel.inf.=0.000  Chi2=**

 3 Habitat
 i Cod Clas  Tot  H(i)  non  act
 0  1  ha1  203  0.55  154  31
 1  2  ha2   93  0.68   0   0
 2  3  ha3  821  0.68   0   0
 3  4  ha4   54  0.59   0   0
 4  5  ha5   61  0.67   0   0
 5  6  ha6  219  0.68   0   0
 6  7  ha7   89  0.61   0   0
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio= 0.00  Rel.inf.=0.000  Chi2=**

**************************************************
 Step #  3 Sub-set #  1 of  26  Sub-set_id#2001000
 No sites:  185;  Entropy:  0.45
  non  act
  154   31
 Sub-set's characteristics :
 ha1  di0
 Terminal sub-set # 1

 2 Distance
 i Cod Clas  Tot  H(i)  non  act
 1  1  di1   23  0.65   0  17
 2  2  di2   31  0.53   0   0
 3  3  di3   19  0.51   0   0
 4  4  di4   16  0.23   0   0
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio= 0.00  Rel.inf.=0.000  Chi2=**

 3 Habitat
 i Cod Clas  Tot  H(i)  non  act
 0  1  ha1  203  0.55   0  17
 1  2  ha2   93  0.68   0   0
 2  3  ha3  821  0.68   0   0
 3  4  ha4   54  0.59   0   0
 4  5  ha5   61  0.67   0   0
 5  6  ha6  219  0.68   0   0
 6  7  ha7   89  0.61   0   0
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio= 0.00  Rel.inf.=0.000  Chi2=**

**************************************************
 Step #  3 Sub-set #  2 of  26  Sub-set_id#2002000
 No sites:   17;  Entropy:  0.00
  non  act
```

```
  0  17
 Sub-set's characteristics :
 ha1  di1
 Terminal sub-set # 2

 2 Distance
 i Cod Clas  Tot  H(i)  non  act
 1  1  di1   23  0.65   0   0
 2  2  di2   31  0.53   0   1
 3  3  di3   19  0.51   0   0
 4  4  di4   16  0.23   0   0
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio= 0.00  Rel.inf.=0.000  Chi2=**

 3 Habitat
 i Cod Clas  Tot  H(i)  non  act
 0  1  ha1  203  0.55   0   1
 1  2  ha2   93  0.68   0   0
 2  3  ha3  821  0.68   0   0
 3  4  ha4   54  0.59   0   0
 4  5  ha5   61  0.67   0   0
 5  6  ha6  219  0.68   0   0
 6  7  ha7   89  0.61   0   0
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio= 0.00  Rel.inf.=0.000  Chi2=**

************************************************
 Step #  3 Sub-set #  3 of  26  Sub-set_id#2003000
 No sites:     1;  Entropy:  0.00
  non  act
   0    1
 Sub-set's characteristics :
 ha1  di2
 Terminal sub-set # 3

 2 Distance
 i Cod Clas  Tot  H(i)  non  act
 1  1  di1   23  0.65   0   7
 2  2  di2   31  0.53   0   0
 3  3  di3   19  0.51   0   0
 4  4  di4   16  0.23   0   0
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio= 0.00  Rel.inf.=0.000  Chi2=**

 3 Habitat
 i Cod Clas  Tot  H(i)  non  act
 0  1  ha1  203  0.55   0   0
 1  2  ha2   93  0.68   0   7
 2  3  ha3  821  0.68   0   0
 3  4  ha4   54  0.59   0   0
 4  5  ha5   61  0.67   0   0
```

```
 5  6 ha6  219 0.68   0   0
 6  7 ha7   89 0.61   0   0
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio= 0.00  Rel.inf.=0.000  Chi2=**

************************************************
 Step #  3 Sub-set #  4 of  26  Sub-set_id#2004000
 No sites:     7;  Entropy:  0.00
  non  act
   0    7
 Sub-set's characteristics :
 ha2  di1
 Terminal sub-set # 4

 2 Distance
 i Cod Clas   Tot  H(i)  non  act
 1   1  di1    23  0.65    0    0
 2   2  di2    31  0.53    8    9
 3   3  di3    19  0.51    0    0
 4   4  di4    16  0.23    0    0
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio= 0.00  Rel.inf.=0.000  Chi2=**

 3 Habitat
 i Cod Clas   Tot  H(i)  non  act
 0   1  ha1   203  0.55    0    0
 1   2  ha2    93  0.68    8    9
 2   3  ha3   821  0.68    0    0
 3   4  ha4    54  0.59    0    0
 4   5  ha5    61  0.67    0    0
 5   6  ha6   219  0.68    0    0
 6   7  ha7    89  0.61    0    0
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio= 0.00  Rel.inf.=0.000  Chi2=**

************************************************
 Step #  3 Sub-set #  5 of  26  Sub-set_id#2005000
 No sites:    17;  Entropy:  0.69
  non  act
   8    9
 Sub-set's characteristics :
 ha2  di2
 Terminal sub-set # 5

 2 Distance
 i Cod Clas   Tot  H(i)  non  act
 1   1  di1    23  0.65    0    0
 2   2  di2    31  0.53    0    0
 3   3  di3    19  0.51   15   12
 4   4  di4    16  0.23    0    0
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio= 0.00  Rel.inf.=0.000  Chi2=**
```

```
 3 Habitat
 i Cod Clas  Tot  H(i)  non  act
 0  1 ha1  203 0.55   0   0
 1  2 ha2   93 0.68  15  12
 2  3 ha3  821 0.68   0   0
 3  4 ha4   54 0.59   0   0
 4  5 ha5   61 0.67   0   0
 5  6 ha6  219 0.68   0   0
 6  7 ha7   89 0.61   0   0
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio= 0.00  Rel.inf.=0.000  Chi2=**

**************************************************
 Step #  3 Sub-set #  6 of  26  Sub-set_id#2006000
 No sites:   27;  Entropy:  0.69
  non  act
   15   12
 Sub-set's characteristics :
 ha2  di3
 Terminal sub-set # 6

 2 Distance
 i Cod Clas  Tot  H(i)  non  act
 1  1 di1   23 0.65   0   0
 2  2 di2   31 0.53   0   0
 3  3 di3   19 0.51   0   0
 4  4 di4   16 0.23  16  26
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio= 0.00  Rel.inf.=0.000  Chi2=**

 3 Habitat
 i Cod Clas  Tot  H(i)  non  act
 0  1 ha1  203 0.55   0   0
 1  2 ha2   93 0.68  16  26
 2  3 ha3  821 0.68   0   0
 3  4 ha4   54 0.59   0   0
 4  5 ha5   61 0.67   0   0
 5  6 ha6  219 0.68   0   0
 6  7 ha7   89 0.61   0   0
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio= 0.00  Rel.inf.=0.000  Chi2=**

**************************************************
 Step #  3 Sub-set #  7 of  26  Sub-set_id#2007000
 No sites:   42;  Entropy:  0.66
  non  act
   16   26
 Sub-set's characteristics :
 ha2  di4
 Terminal sub-set # 7
```

```
 2 Distance
 i Cod Clas  Tot  H(i)  non  act
 1   1 di1   23 0.65   0   0
 2   2 di2   31 0.53   0   0
 3   3 di3   19 0.51   0   0
 4   4 di4   16 0.23   0   0
Mut.inf.=0.000 Kulb.= 0.0 S.Ratio= 0.00 Rel.inf.=0.000 Chi2=**

 3 Habitat
 i Cod Clas  Tot  H(i)  non  act
 0   1 ha1  203 0.55   0   0
 1   2 ha2   93 0.68   0   0
 2   3 ha3  821 0.68   0   1
 3   4 ha4   54 0.59   0   0
 4   5 ha5   61 0.67   0   0
 5   6 ha6  219 0.68   0   0
 6   7 ha7   89 0.61   0   0
Mut.inf.=0.000 Kulb.= 0.0 S.Ratio= 0.00 Rel.inf.=0.000 Chi2=**

*************************************************
 Step # 3 Sub-set # 8 of 26 Sub-set_id#2008000
 No sites:    1; Entropy: 0.00
  non  act
   0    1
 Sub-set's characteristics :
 ha3  di0
 Terminal sub-set # 8

 2 Distance
 i Cod Clas  Tot  H(i)  non  act
 1   1 di1   23 0.65  30  70
 2   2 di2   31 0.53   0   0
 3   3 di3   19 0.51   0   0
 4   4 di4   16 0.23   0   0
Mut.inf.=0.000 Kulb.= 0.0 S.Ratio= 0.00 Rel.inf.=0.000 Chi2=**

 3 Habitat
 i Cod Clas  Tot  H(i)  non  act
 0   1 ha1  203 0.55   0   0
 1   2 ha2   93 0.68   0   0
 2   3 ha3  821 0.68  30  70
 3   4 ha4   54 0.59   0   0
 4   5 ha5   61 0.67   0   0
 5   6 ha6  219 0.68   0   0
 6   7 ha7   89 0.61   0   0
Mut.inf.=0.000 Kulb.= 0.0 S.Ratio= 0.00 Rel.inf.=0.000 Chi2=**
```

```
************************************************
 Step # 3 Sub-set # 9 of 26 Sub-set_id#2009000
 No sites:  100; Entropy: 0.61
  non act
   30 70
 Sub-set's characteristics :
 ha3 di1
 Terminal sub-set # 9

 2 Distance
 i Cod Clas  Tot H(i) non act
 1  1 di1   23 0.65   0   0
 2  2 di2   31 0.53  93 165
 3  3 di3   19 0.51   0   0
 4  4 di4   16 0.23   0   0
Mut.inf.=0.000 Kulb.= 0.0 S.Ratio=0.00 Rel.inf.=0.000 Chi2=**

 3 Habitat
 i Cod Clas  Tot H(i) non act
 0  1 ha1  203 0.55   0   0
 1  2 ha2   93 0.68   0   0
 2  3 ha3  821 0.68  93 165
 3  4 ha4   54 0.59   0   0
 4  5 ha5   61 0.67   0   0
 5  6 ha6  219 0.68   0   0
 6  7 ha7   89 0.61   0   0
Mut.inf.=0.000 Kulb.= 0.0 S.Ratio=0.00 Rel.inf.=0.000 Chi2=**

************************************************
 Step # 3 Sub-set # 10 of 26 Sub-set_id#2010000
 No sites:  258; Entropy: 0.65
  non act
   93 165
 Sub-set's characteristics :
 ha3 di2
 Terminal sub-set # 10

 2 Distance
 i Cod Clas  Tot H(i) non act
 1  1 di1   23 0.65   0   0
 2  2 di2   31 0.53   0   0
 3  3 di3   19 0.51 108 137
 4  4 di4   16 0.23   0   0
Mut.inf.=0.000 Kulb.= 0.0 S.Ratio=0.00 Rel.inf.=0.000 Chi2=**

 3 Habitat
 i Cod Clas  Tot H(i) non act
 0  1 ha1  203 0.55   0   0
```

```
 1  2 ha2   93 0.68   0   0
 2  3 ha3  821  0.68  108  137
 3  4 ha4   54 0.59   0   0
 4  5 ha5   61 0.67   0   0
 5  6 ha6  219 0.68   0   0
 6  7 ha7   89 0.61   0   0
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio= 0.00  Rel.inf.=0.000  Chi2=**

************************************************
 Step #  3 Sub-set # 11 of  26  Sub-set_id#2011000
 No sites:  245;  Entropy:  0.69
  non  act
  108  137
 Sub-set's characteristics :
 ha3  di3
 Terminal sub-set # 11

 2 Distance
 i Cod Clas   Tot  H(i)  non  act
 1   1 di1    23 0.65   0   0
 2   2 di2    31 0.53   0   0
 3   3 di3    19 0.51   0   0
 4   4 di4    16 0.23  108  109
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio= 0.00  Rel.inf.=0.000  Chi2=**

 3 Habitat
 i Cod Clas   Tot  H(i)  non  act
 0   1 ha1   203 0.55   0   0
 1   2 ha2    93 0.68   0   0
 2   3 ha3   821  0.68  108  109
 3   4 ha4    54 0.59   0   0
 4   5 ha5    61 0.67   0   0
 5   6 ha6   219 0.68   0   0
 6   7 ha7    89 0.61   0   0
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio= 0.00  Rel.inf.=0.000  Chi2=**

************************************************
 Step #  3 Sub-set # 12 of  26  Sub-set_id#2012000
 No sites:  217;  Entropy:  0.69
  non  act
  108  109
 Sub-set's characteristics :
 ha3  di4
 Terminal sub-set # 12

 2 Distance
 i Cod Clas   Tot  H(i)  non  act
 1   1 di1    23 0.65   0   0
```

```
 2  2 di2   31 0.53  0  0
 3  3 di3   19 0.51  0  0
 4  4 di4   16 0.23  0  0
Mut.inf.=0.000 Kulb.= 0.0 S.Ratio=0.00 Rel.inf.=0.000 Chi2=**

 3 Habitat
 i Cod Clas  Tot H(i) non act
 0  1 ha1  203 0.55  0  0
 1  2 ha2   93 0.68  0  0
 2  3 ha3  821 0.68  0  0
 3  4 ha4   54 0.59  0  0
 4  5 ha5   61 0.67  0  1
 5  6 ha6  219 0.68  0  0
 6  7 ha7   89 0.61  0  0
Mut.inf.=0.000 Kulb.= 0.0 S.Ratio=0.00 Rel.inf.=0.000 Chi2=**

**************************************************
 Step # 3 Sub-set # 13 of 26 Sub-set_id#2013000
 No sites:   1; Entropy: 0.00
  non act
   0   1
 Sub-set's characteristics :
 ha5 di0
 Terminal sub-set # 13

 2 Distance
 i Cod Clas  Tot H(i) non act
 1  1 di1   23 0.65  8 17
 2  2 di2   31 0.53  0  0
 3  3 di3   19 0.51  0  0
 4  4 di4   16 0.23  0  0
Mut.inf.=0.000 Kulb.= 0.0 S.Ratio=0.00 Rel.inf.=0.000 Chi2=**

 3 Habitat
 i Cod Clas  Tot H(i) non act
 0  1 ha1  203 0.55  0  0
 1  2 ha2   93 0.68  0  0
 2  3 ha3  821 0.68  0  0
 3  4 ha4   54 0.59  0  0
 4  5 ha5   61 0.67  8 17
 5  6 ha6  219 0.68  0  0
 6  7 ha7   89 0.61  0  0
Mut.inf.=0.000 Kulb.= 0.0 S.Ratio=0.00 Rel.inf.=0.000 Chi2=**

**************************************************
 Step # 3 Sub-set # 14 of 26 Sub-set_id#2014000
 No sites:   25; Entropy: 0.63
  non act
```

```
  8  17
 Sub-set's characteristics :
 ha5  di1
 Terminal sub-set # 14

 2 Distance
 i Cod Clas   Tot  H(i)  non  act
 1   1  di1    23  0.65   0    0
 2   2  di2    31  0.53  15    5
 3   3  di3    19  0.51   0    0
 4   4  di4    16  0.23   0    0
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio=0.00  Rel.inf.=0.000  Chi2=**

 3 Habitat
 i Cod Clas   Tot  H(i)  non  act
 0   1  ha1   203  0.55   0    0
 1   2  ha2    93  0.68   0    0
 2   3  ha3   821  0.68   0    0
 3   4  ha4    54  0.59   0    0
 4   5  ha5    61  0.67  15    5
 5   6  ha6   219  0.68   0    0
 6   7  ha7    89  0.61   0    0
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio=0.00  Rel.inf.=0.000  Chi2=**

**************************************************
 Step #  3 Sub-set # 15 of  26  Sub-set_id#2015000
 No sites:   20;  Entropy:  0.56
  non  act
   15   5
 Sub-set's characteristics :
 ha5  di2
 Terminal sub-set # 15

 2 Distance
 i Cod Clas   Tot  H(i)  non  act
 1   1  di1    23  0.65   0    0
 2   2  di2    31  0.53   0    0
 3   3  di3    19  0.51   7    0
 4   4  di4    16  0.23   0    0
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio=0.00  Rel.inf.=0.000  Chi2=**

 3 Habitat
 i Cod Clas   Tot  H(i)  non  act
 0   1  ha1   203  0.55   0    0
 1   2  ha2    93  0.68   0    0
 2   3  ha3   821  0.68   0    0
 3   4  ha4    54  0.59   0    0
 4   5  ha5    61  0.67   7    0
```

```
 5  6  ha6   219 0.68   0   0
 6  7  ha7    89 0.61   0   0
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio= 0.00  Rel.inf.=0.000  Chi2=**

**************************************************
 Step #  3 Sub-set # 16 of  26  Sub-set_id#2016000
 No sites:    7;  Entropy:  0.00
  non  act
   7    0
 Sub-set's characteristics :
 ha5  di3
 Terminal sub-set # 16

 2 Distance
 i Cod Clas   Tot  H(i)  non  act
 1   1  di1    23  0.65   0    0
 2   2  di2    31  0.53   0    0
 3   3  di3    19  0.51   0    0
 4   4  di4    16  0.23   7    1
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio= 0.00  Rel.inf.=0.000  Chi2=**

 3 Habitat
 i Cod Clas   Tot  H(i)  non  act
 0   1  ha1   203  0.55   0    0
 1   2  ha2    93  0.68   0    0
 2   3  ha3   821  0.68   0    0
 3   4  ha4    54  0.59   0    0
 4   5  ha5    61  0.67   7    1
 5   6  ha6   219  0.68   0    0
 6   7  ha7    89  0.61   0    0
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio= 0.00  Rel.inf.=0.000  Chi2=**

**************************************************
 Step #  3 Sub-set # 17 of  26  Sub-set_id#2017000
 No sites:    8;  Entropy:  0.38
  non  act
   7    1
 Sub-set's characteristics :
 ha5  di4
 Terminal sub-set # 17

 2 Distance
 i Cod Clas   Tot  H(i)  non  act
 1   1  di1    23  0.65   0    0
 2   2  di2    31  0.53   0    0
 3   3  di3    19  0.51   0    0
 4   4  di4    16  0.23   0    0
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio= 0.00  Rel.inf.=0.000  Chi2=**
```

```
 3 Habitat
 i Cod Clas  Tot  H(i)  non  act
 0   1  ha1   203  0.55    0    0
 1   2  ha2    93  0.68    0    0
 2   3  ha3   821  0.68    0    0
 3   4  ha4    54  0.59    0    0
 4   5  ha5    61  0.67    0    0
 5   6  ha6   219  0.68    0    6
 6   7  ha7    89  0.61    0    0
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio=0.00  Rel.inf.=0.000  Chi2=**

**************************************************
 Step #  3 Sub-set # 18 of  26  Sub-set_id#2018000
 No sites:    6;  Entropy:  0.00
  non  act
   0    6
 Sub-set's characteristics :
 ha6  di0
 Terminal sub-set # 18

 2 Distance
 i Cod Clas  Tot  H(i)  non  act
 1   1  di1    23  0.65   93   65
 2   2  di2    31  0.53    0    0
 3   3  di3    19  0.51    0    0
 4   4  di4    16  0.23    0    0
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio=0.00  Rel.inf.=0.000  Chi2=**

 3 Habitat
 i Cod Clas  Tot  H(i)  non  act
 0   1  ha1   203  0.55    0    0
 1   2  ha2    93  0.68    0    0
 2   3  ha3   821  0.68    0    0
 3   4  ha4    54  0.59    0    0
 4   5  ha5    61  0.67    0    0
 5   6  ha6   219  0.68   93   65
 6   7  ha7    89  0.61    0    0
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio=0.00  Rel.inf.=0.000  Chi2=**

**************************************************
 Step #  3 Sub-set # 19 of  26  Sub-set_id#2019000
 No sites:  158;  Entropy:  0.68
  non  act
   93   65
 Sub-set's characteristics :
 ha6  di1
 Terminal sub-set # 19
```

```
 2 Distance
 i Cod Clas  Tot  H(i)  non  act
 1  1  di1   23  0.65   0    0
 2  2  di2   31  0.53  14    8
 3  3  di3   19  0.51   0    0
 4  4  di4   16  0.23   0    0
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio= 0.00  Rel.inf.=0.000  Chi2=**

 3 Habitat
 i Cod Clas  Tot  H(i)  non  act
 0  1  ha1  203  0.55   0    0
 1  2  ha2   93  0.68   0    0
 2  3  ha3  821  0.68   0    0
 3  4  ha4   54  0.59   0    0
 4  5  ha5   61  0.67   0    0
 5  6  ha6  219  0.68  14    8
 6  7  ha7   89  0.61   0    0
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio= 0.00  Rel.inf.=0.000  Chi2=**

************************************************
 Step #  3 Sub-set # 20 of  26  Sub-set_id#2020000
 No sites:   22;  Entropy:  0.66
  non  act
   14   8
 Sub-set's characteristics :
 ha6  di2
 Terminal sub-set # 20

 2 Distance
 i Cod Clas  Tot  H(i)  non  act
 1  1  di1   23  0.65   0    0
 2  2  di2   31  0.53   0    0
 3  3  di3   19  0.51   9   11
 4  4  di4   16  0.23   0    0
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio= 0.00  Rel.inf.=0.000  Chi2=**

 3 Habitat
 i Cod Clas  Tot  H(i)  non  act
 0  1  ha1  203  0.55   0    0
 1  2  ha2   93  0.68   0    0
 2  3  ha3  821  0.68   0    0
 3  4  ha4   54  0.59   0    0
 4  5  ha5   61  0.67   0    0
 5  6  ha6  219  0.68   9   11
 6  7  ha7   89  0.61   0    0
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio= 0.00  Rel.inf.=0.000  Chi2=**
```

```
************************************************
 Step # 3 Sub-set # 21 of 26 Sub-set_id#2021000
 No sites:  20; Entropy: 0.69
  non act
   9  11
 Sub-set's characteristics :
 ha6 di3
 Terminal sub-set # 21

 2 Distance
 i Cod Clas  Tot H(i) non act
 1  1 di1   23 0.65  0  0
 2  2 di2   31 0.53  0  0
 3  3 di3   19 0.51  0  0
 4  4 di4   16 0.23  8  5
Mut.inf.=0.000 Kulb.= 0.0 S.Ratio= 0.00 Rel.inf.=0.000 Chi2=**

 3 Habitat
 i Cod Clas  Tot H(i) non act
 0  1 ha1  203 0.55  0  0
 1  2 ha2   93 0.68  0  0
 2  3 ha3  821 0.68  0  0
 3  4 ha4   54 0.59  0  0
 4  5 ha5   61 0.67  0  0
 5  6 ha6  219 0.68  8  5
 6  7 ha7   89 0.61  0  0
Mut.inf.=0.000 Kulb.= 0.0 S.Ratio= 0.00 Rel.inf.=0.000 Chi2=**

************************************************
 Step # 3 Sub-set # 22 of 26 Sub-set_id#2022000
 No sites:  13; Entropy: 0.67
  non act
   8  5
 Sub-set's characteristics :
 ha6 di4
 Terminal sub-set # 22

 2 Distance
 i Cod Clas  Tot H(i) non act
 1  1 di1   23 0.65  8 15
 2  2 di2   31 0.53  0  0
 3  3 di3   19 0.51  0  0
 4  4 di4   16 0.23  0  0
Mut.inf.=0.000 Kulb.= 0.0 S.Ratio= 0.00 Rel.inf.=0.000 Chi2=**

 3 Habitat
 i Cod Clas  Tot H(i) non act
 0  1 ha1  203 0.55  0  0
```

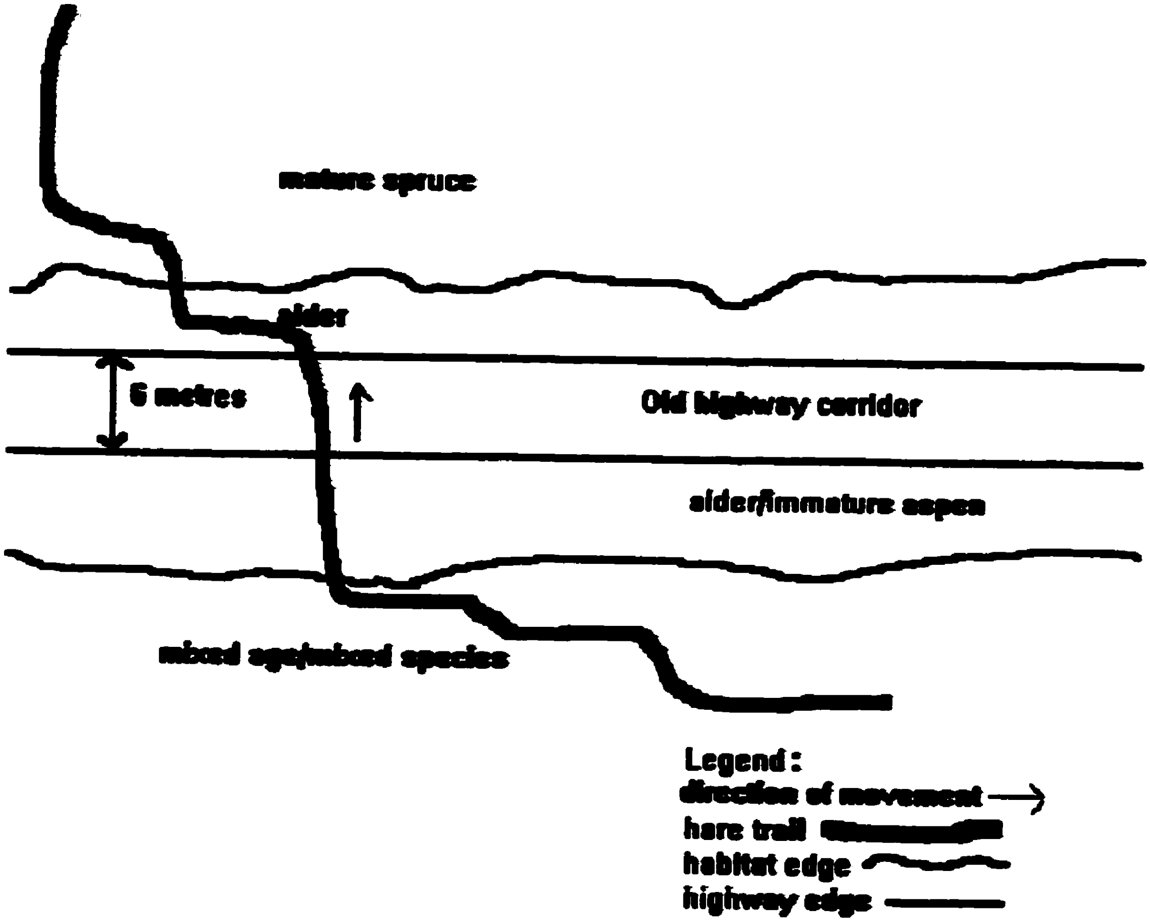
```
 1  2 ha2   93 0.68  0  0
 2  3 ha3  821 0.68  0  0
 3  4 ha4   54 0.59  0  0
 4  5 ha5   61 0.67  0  0
 5  6 ha6  219 0.68  0  0
 6  7 ha7   89 0.61  8  15
Mut.inf.=0.000 Kulb.= 0.0 S.Ratio= 0.00 Rel.inf.=0.000 Chi2=**

**************************************************
 Step #  3 Sub-set # 23 of  26  Sub-set_id#2023000
 No sites:   23;  Entropy:  0.65
  non  act
   8  15
 Sub-set's characteristics :
 ha7  di1
 Terminal sub-set # 23

 2 Distance
 i Cod Clas   Tot  H(i)  non  act
 1  1 di1   23 0.65  0  0
 2  2 di2   31 0.53  24  7
 3  3 di3   19 0.51  0  0
 4  4 di4   16 0.23  0  0
Mut.inf.=0.000 Kulb.= 0.0 S.Ratio= 0.00 Rel.inf.=0.000 Chi2=**

 3 Habitat
 i Cod Clas   Tot  H(i)  non  act
 0  1 ha1  203 0.55  0  0
 1  2 ha2   93 0.68  0  0
 2  3 ha3  821 0.68  0  0
 3  4 ha4   54 0.59  0  0
 4  5 ha5   61 0.67  0  0
 5  6 ha6  219 0.68  0  0
 6  7 ha7   89 0.61  24  7
Mut.inf.=0.000 Kulb.= 0.0 S.Ratio= 0.00 Rel.inf.=0.000 Chi2=**

**************************************************
 Step #  3 Sub-set # 24 of  26  Sub-set_id#2024000
 No sites:   31;  Entropy:  0.53
  non  act
  24   7
 Sub-set's characteristics :
 ha7  di2
 Terminal sub-set # 24

 2 Distance
 i Cod Clas   Tot  H(i)  non  act
 1  1 di1   23 0.65  0  0
```

```
 2  2 di2   31 0.53   0   0
 3  3 di3   19 0.51  15   4
 4  4 di4   16 0.23   0   0
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio= 0.00  Rel.inf.=0.000  Chi2=**

 3 Habitat
 i Cod Clas   Tot  H(i)  non  act
 0   1  ha1   203  0.55   0   0
 1   2  ha2    93  0.68   0   0
 2   3  ha3   821  0.68   0   0
 3   4  ha4    54  0.59   0   0
 4   5  ha5    61  0.67   0   0
 5   6  ha6   219  0.68   0   0
 6   7  ha7    89  0.61  15   4
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio= 0.00  Rel.inf.=0.000  Chi2=**

**************************************************
 Step #  3 Sub-set # 25 of  26  Sub-set_id#2025000
 No sites:    19;  Entropy:  0.51
  non  act
   15   4
 Sub-set's characteristics :
 ha7  di3
 Terminal sub-set # 25

 2 Distance
 i Cod Clas   Tot  H(i)  non  act
 1   1  di1    23  0.65   0   0
 2   2  di2    31  0.53   0   0
 3   3  di3    19  0.51   0   0
 4   4  di4    16  0.23  15   1
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio= 0.00  Rel.inf.=0.000  Chi2=**

 3 Habitat
 i Cod Clas   Tot  H(i)  non  act
 0   1  ha1   203  0.55   0   0
 1   2  ha2    93  0.68   0   0
 2   3  ha3   821  0.68   0   0
 3   4  ha4    54  0.59   0   0
 4   5  ha5    61  0.67   0   0
 5   6  ha6   219  0.68   0   0
 6   7  ha7    89  0.61  15   1
Mut.inf.=0.000  Kulb.=  0.0  S.Ratio= 0.00  Rel.inf.=0.000  Chi2=**

**************************************************
 Step #  3 Sub-set # 26 of  26  Sub-set_id#2026000
 No sites:    16;  Entropy:  0.23
  non  act
```

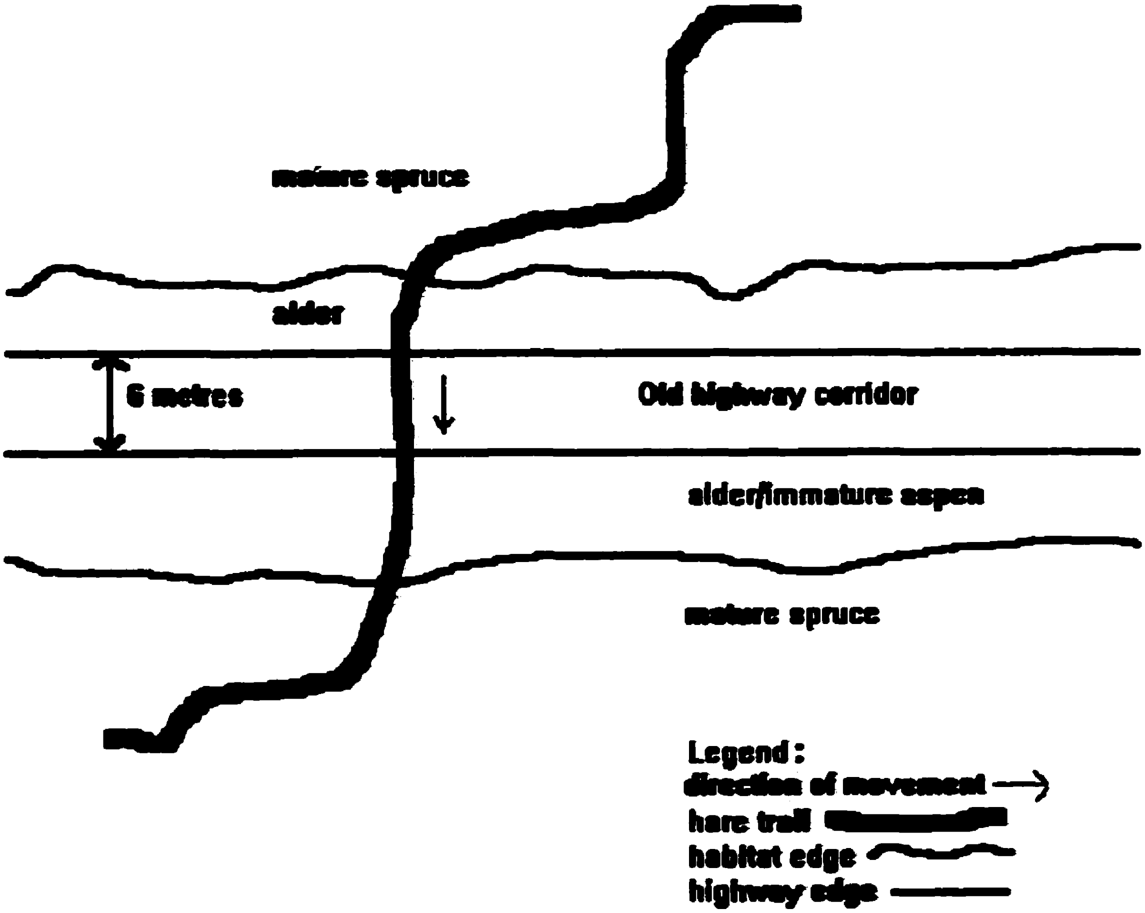
```
  15   1
 Sub-set's characteristics :
 ha7  di4
 Terminal sub-set # 26

Matrix    27 TSS x Depdendent variable
   1  15  39   54
   2 154  31  185
   3   0  17   17
   4   0   1    1
   5   0   7    7
   6   8   9   17
   7  15  12   27
   8  16  26   42
   9   0   1    1
  10  30  70  100
  11  93 165  258
  12 108 137  245
  13 108 109  217
  14   0   1    1
  15   8  17   25
  16  15   5   20
  17   7   0    7
  18   7   1    8
  19   0   6    6
  20  93  65  158
  21  14   8   22
  22   9  11   20
  23   8   5   13
  24   8  15   23
  25  24   7   31
  26  15   4   19
  27  15   1   16

 Environmental specificity
 0.119 0.119


 Variable's contribution to the negentropy

 # 2 Var.name:    Distance  Init.cont.=0.03  Fin.cont.=0.04  p.cent=54.1
 # 3 Var.name:     Habitat  Init.cont.=0.04  Fin.cont.=0.04  p.cent= 45.9


Entropy change as a function of the number of subsets

 Div.# 0 No.Subsets=  1  H(U/E)=0.693  H(E)=0.000
 Div.# 1 No.Subsets=  7  H(U/E)=0.655  H(E)=1.459
```

```
 Div.# 2 No.Subsets=  9  H(U/E)=0.637  H(E)=1.501
 Div.# 3 No.Subsets= 12  H(U/E)=0.634  H(E)=1.575
 Div.# 4 No.Subsets= 16  H(U/E)=0.628  H(E)=2.290
 Div.# 5 No.Subsets= 20  H(U/E)=0.621  H(E)=2.342
 Div.# 6 No.Subsets= 24  H(U/E)=0.617  H(E)=2.477
 Div.# 7 No.Subsets= 27  H(U/E)=0.611  H(E)=2.556


Initial entropy: 0.693         Final entropy: 0.611
Negentropy: 0.082   Redundancy:  11.9p.c. for  27 TSS
Adj.negen.: 0.092   Adj.redun.:  13.3p.c.   (r2=0.969)
Adj.function: H(u/e) = exp(-0.077*TSS -2.415) + 0.601

Environment entr.: 2.556   Adj.entr.: 3.268 ( 54 TSS)
Adj.function: H(e) = ln(0.476*TSS 0.561)   (r2=0.957)

!!! Total data memory alloc.= 44 kbytes !!!
```

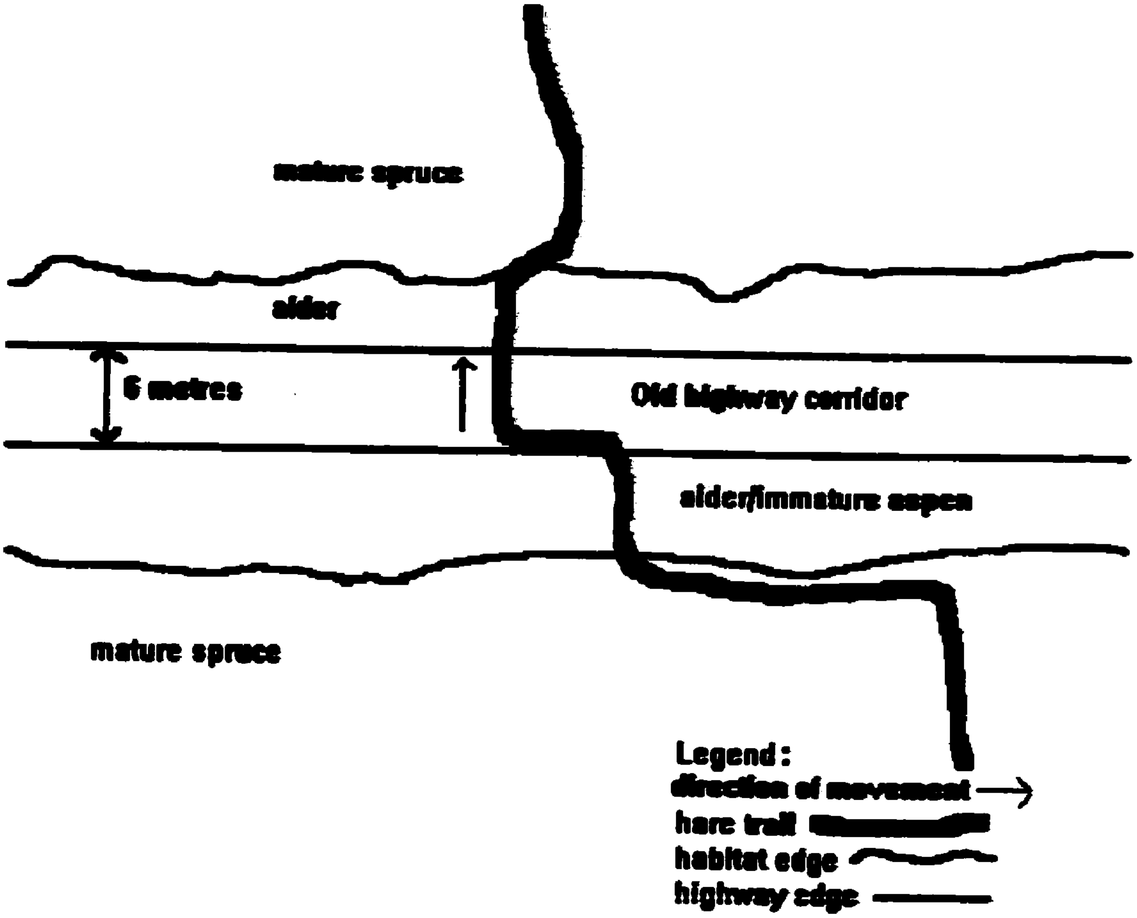
CASE 1


mature spruce
alder
6 metres
Old highway corridor
alder/immature aspen
mixed age/mixed species
Legend:
direction of movement
hare trail
habitat edge
highway edge

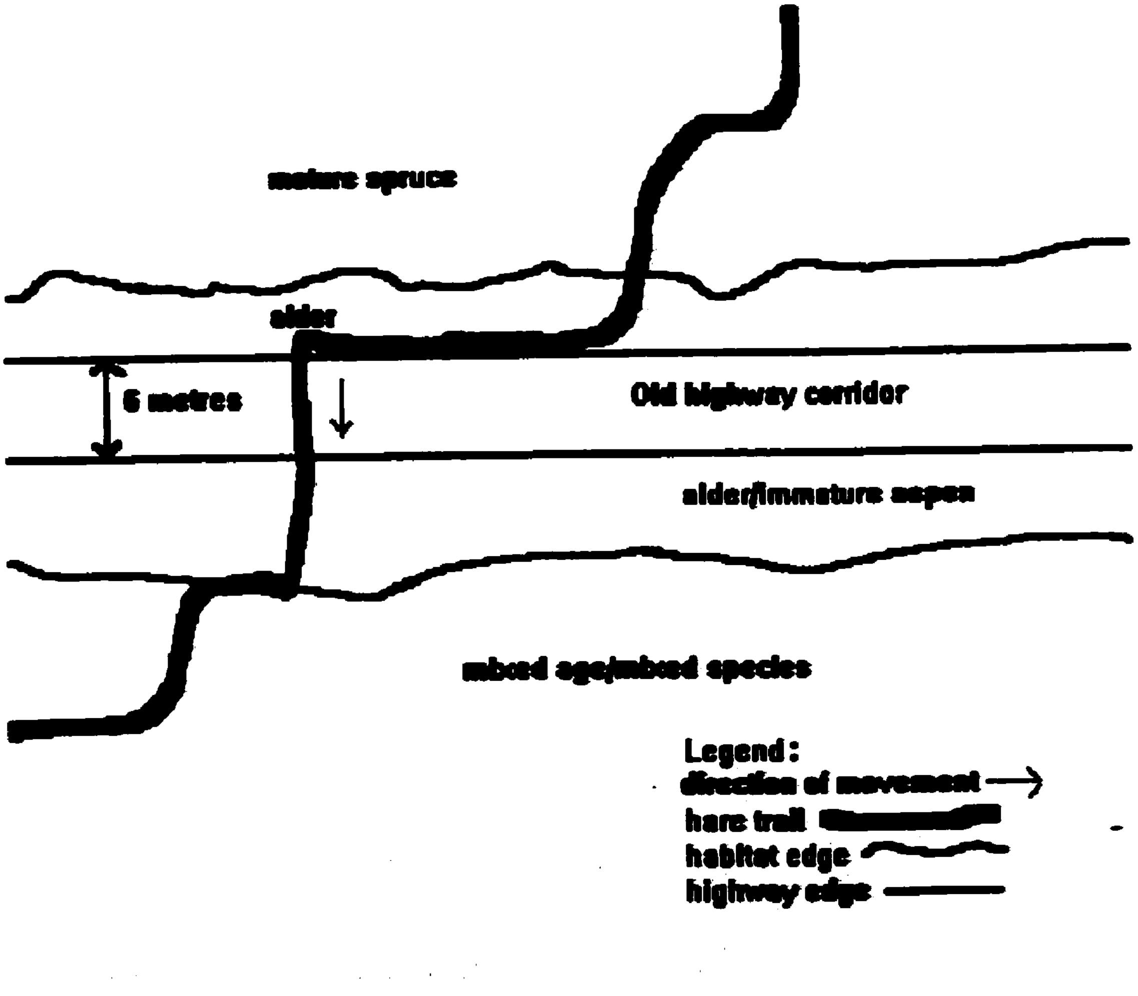
CASE 2

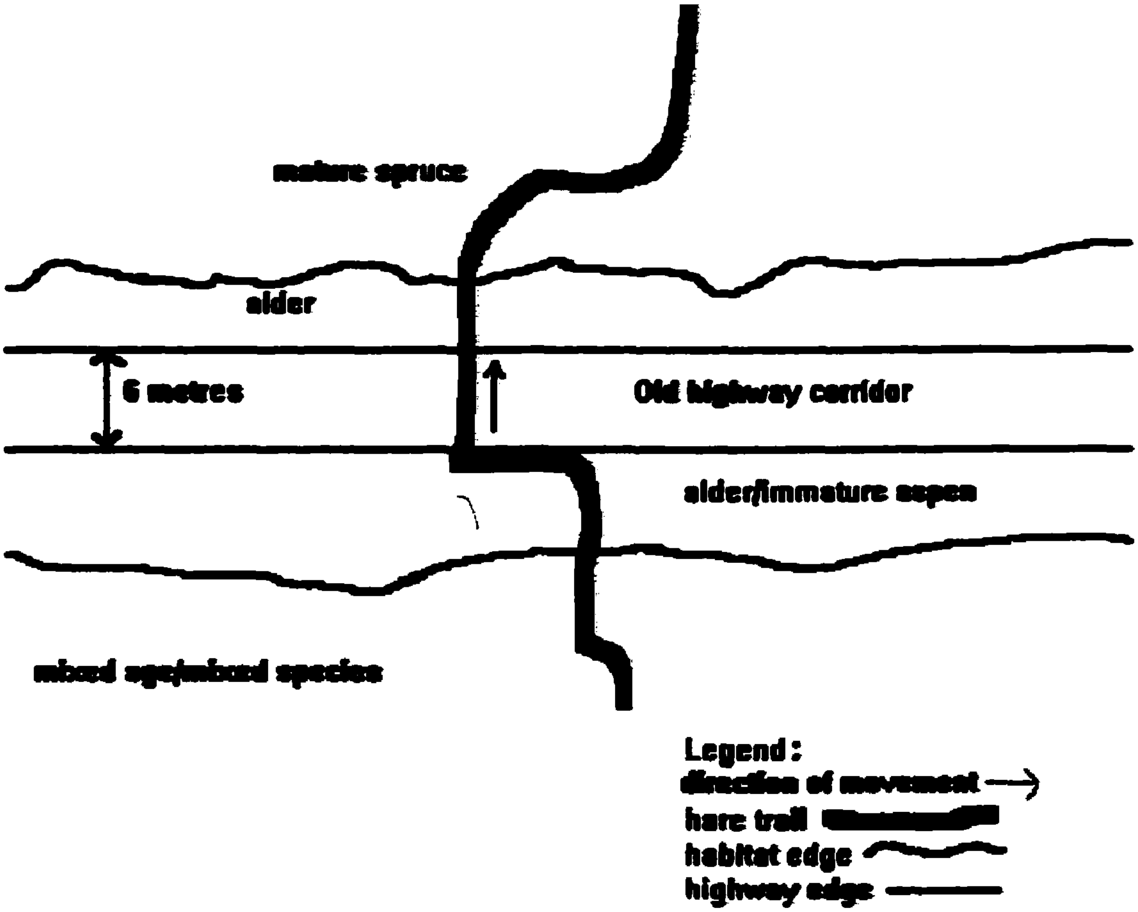

mature spruce
alder
6 metres
Old highway corridor
alder/immature aspen
mature spruce
Legend:
direction of movement
hare trail
habitat edge
highway edge

CASE3

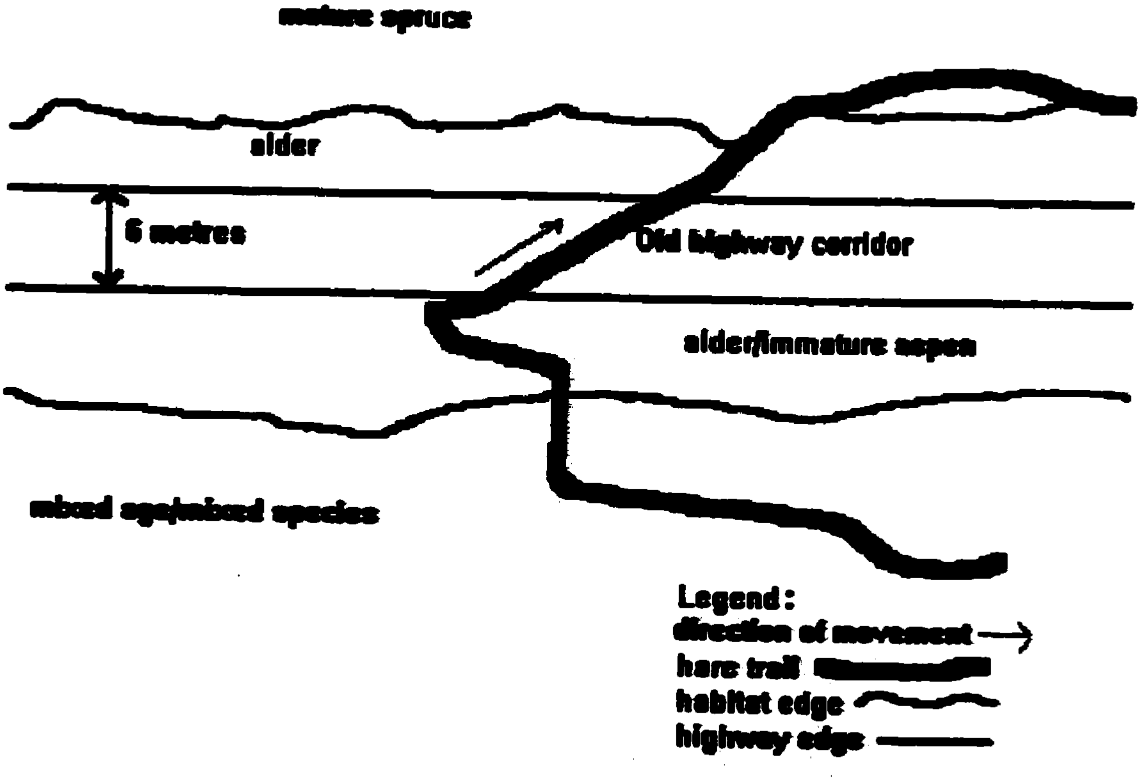

mature spruce
alder
6 metres
Old highway corridor
alder/immature aspen
mature spruce
Legend:
direction of movement →
hare trail
habitat edge
highway edge

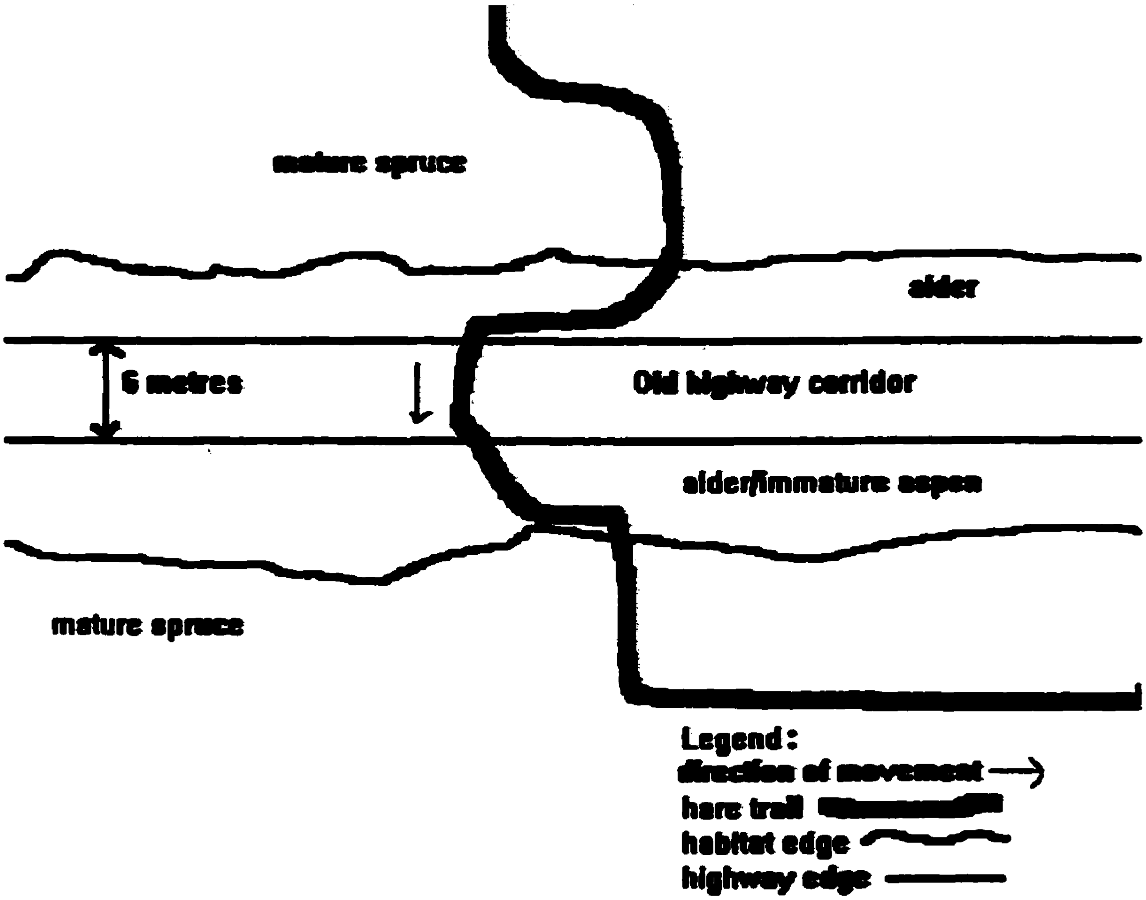
CASE 4


mature spruce
alder
6 metres
Old highway corridor
alder/immature aspen
mixed age/mixed species
Legend:
direction of movement →
hare trail
habitat edge
highway edge

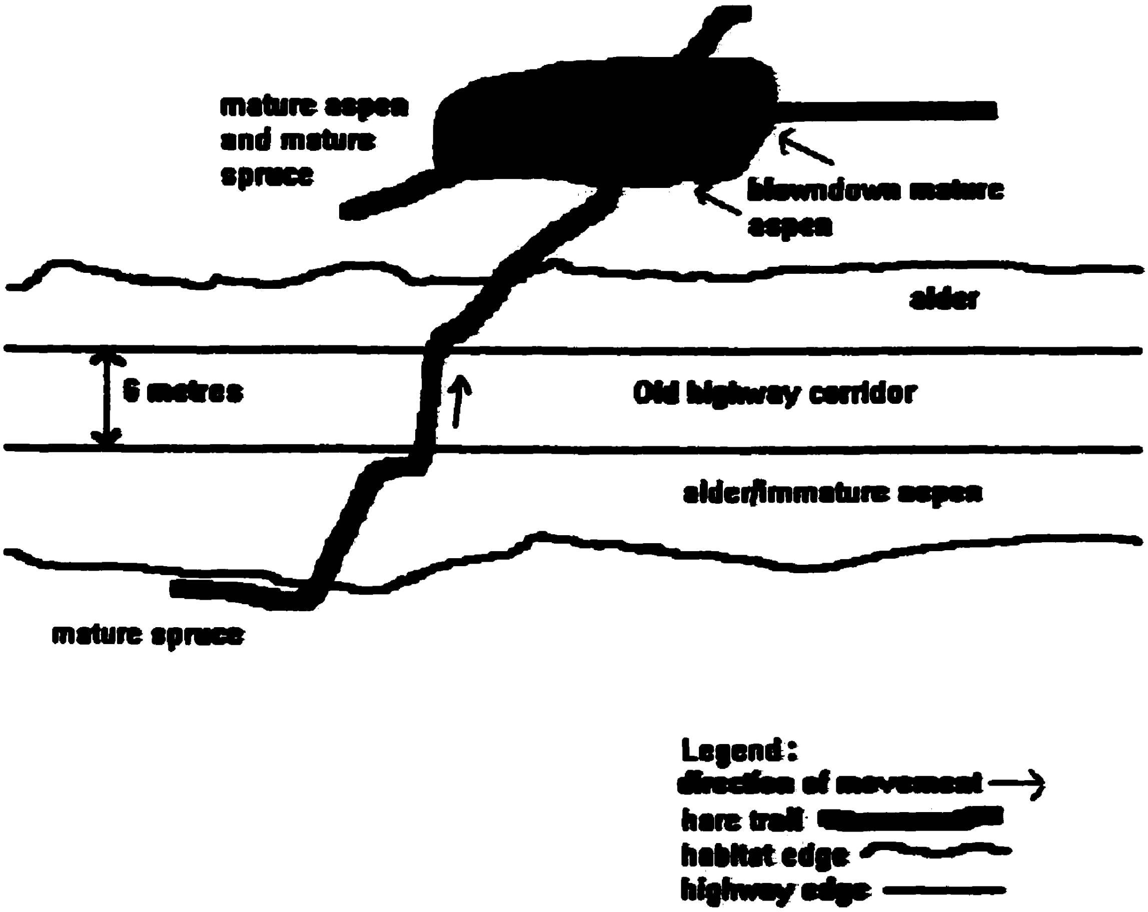

mature spruce
alder
6 metres
Old highway corridor
alder/immature aspen
mixed age/mixed species
Legend:
direction of movement
hare trail
habitat edge
highway edge

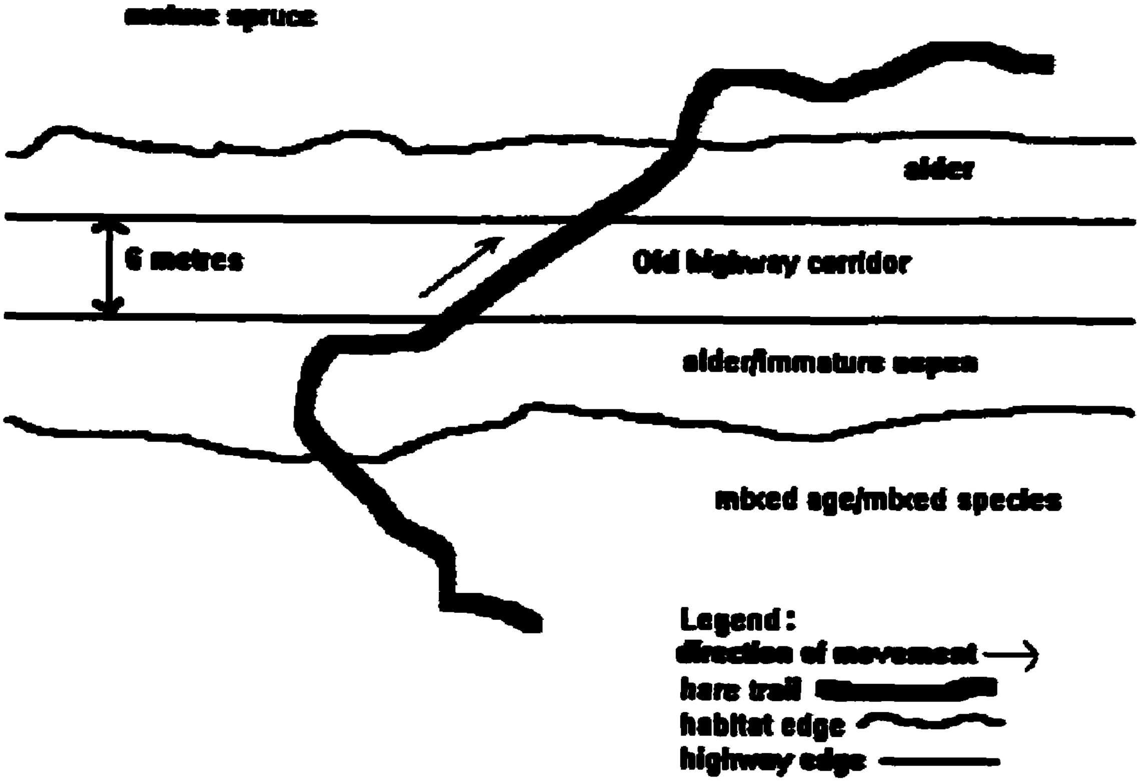
CASE 6


mature spruce
alder
6 metres
Old highway corridor
alder/immature aspen
mixed age/mixed species
Legend:
direction of movement
hare trail
habitat edge
highway edge


mature spruce
alder
6 metres
Old highway corridor
alder/immature aspen
mature spruce
Legend:
direction of movement →
hare trail
habitat edge
highway edge

CASE 8


mature aspen and mature spruce
blowdown mature aspen
alder
6 metres
Old highway corridor
alder/immature aspen
mature spruce
Legend:
direction of movement →
hare trail
habitat edge
highway edge


mature spruce
alder
6 metres
Old highway corridor
alder/immature aspen
mixed age/mixed species
Legend:
direction of movement
hare trail
habitat edge
highway edge

CASE 10

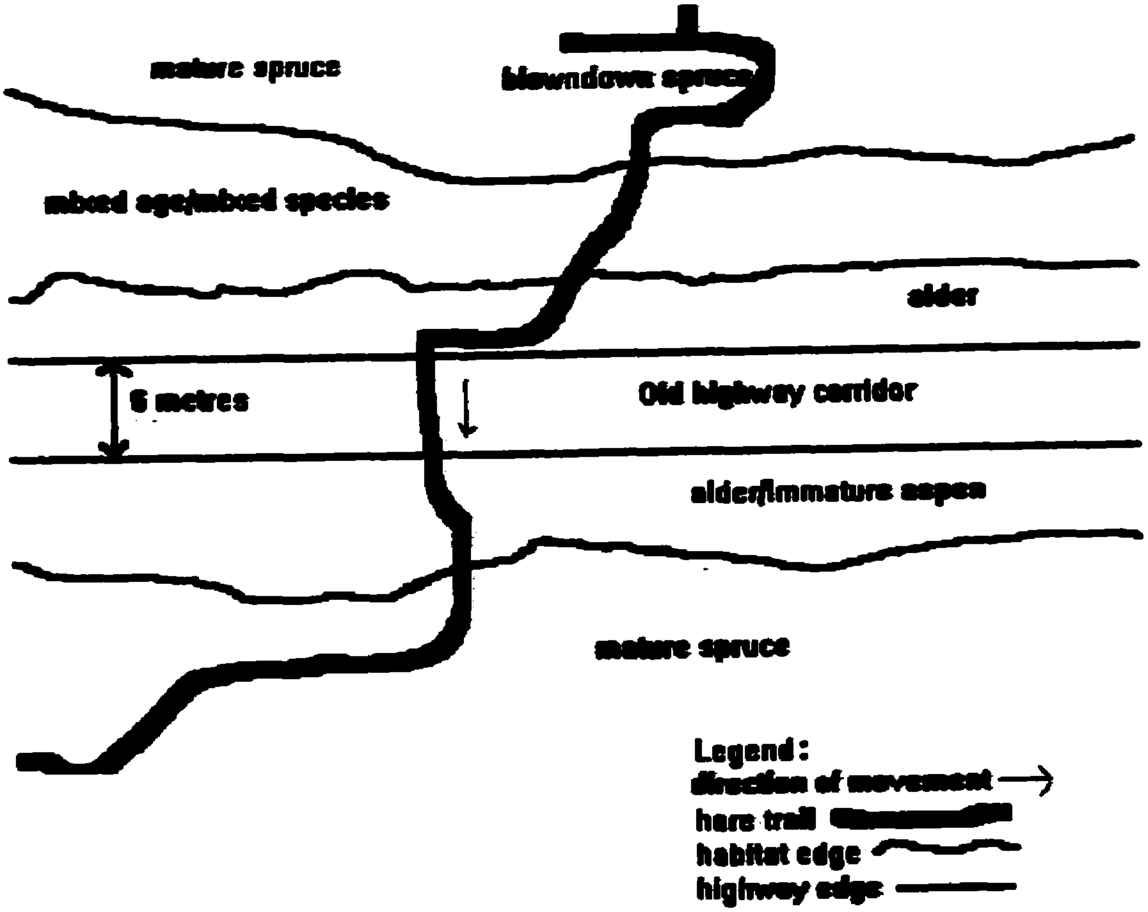

mature spruce
blowndown spruce
mixed age/mixed species
alder
6 metres
Old highway corridor
alder/immature aspen
mature spruce
Legend:
direction of movement
hare trail
habitat edge
highway edge

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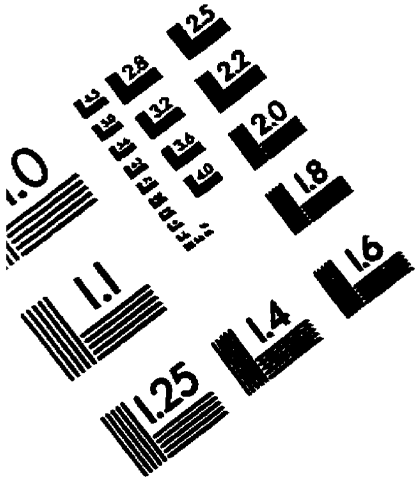
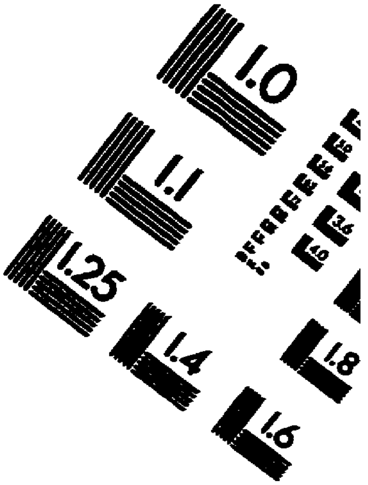
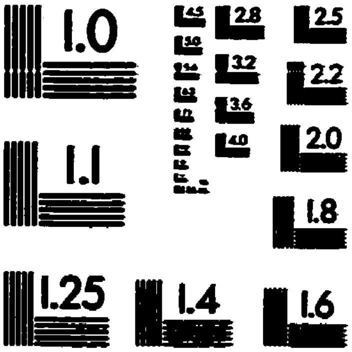
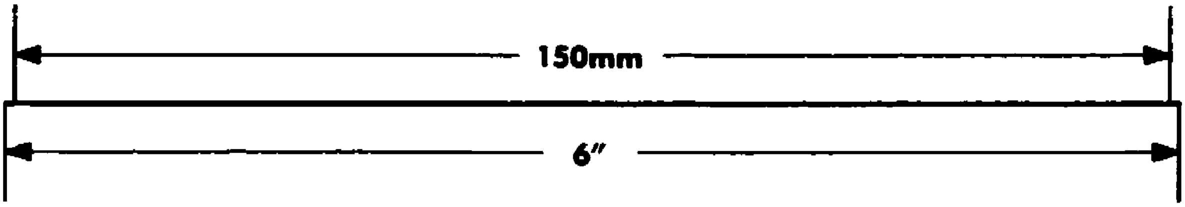
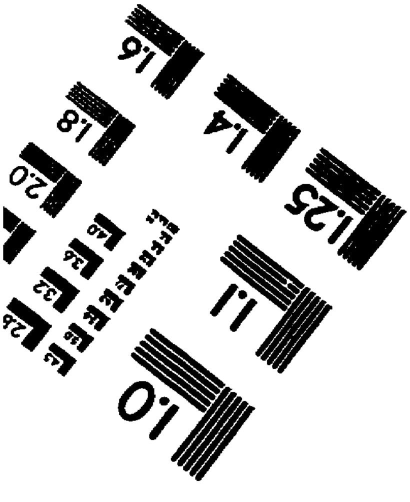
IMAGE EVALUATION TEST TARGET (QA-3)











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